

ACOUSTIC SEXUAL COMMUNICATION IN THE HOUSE CRICKET (*ACHETA*
DOMESTICUS) : EFFECTS OF FEMALE CHOICE AND INTERMALE
COMPETITION ON MALE CALLING SONG

by

Rebecca Michelle Sorensen Sage

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A Dissertation Submitted to the Faculty of the

DEPARTMENT OF PSYCHOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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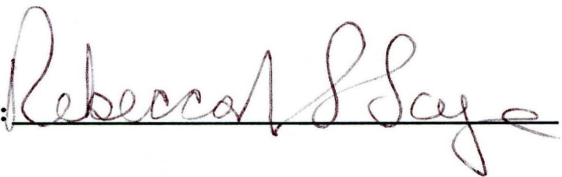
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A handwritten signature in dark ink, appearing to read "Rebecca S. Saye", is written over a horizontal line.

ACKNOWLEDGMENTS

I would like to thank my dissertation director, A. J. Figueredo for all his guidance and instruction throughout my graduate career. I would like to thank my committee members, Mary Wetzel, Jim King, Terry Daniel, and David Rowe for all their thoughtful comments, remarks, and critiques of earlier drafts of this dissertation. Also, much thanks goes out to all of the students that dedicated time to collecting and entering the data for this experiment.

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ABSTRACT

This dissertation reports on a study conducted to examine the morphological, behavioral, and environmental sources of variation in the structure of house cricket, *Acheta domesticus*, calling song. Song variations may be important in female mating decisions and influence male mating success. Eleven song parameters were measured: chirp duration, interchirp duration, syllable number, syllable duration, intersyllable duration, mean frequency, frequency intensity, minimum frequency, maximum frequency, syllable intensity, and intensity difference between syllable and frequency intensity. Morphological factors examined included body: mass, length, color, asymmetry, intactness; and male age. Behavioral factors were timing of song bouts and proclivity to sing. Environmental conditions of high population densities were simulated by temporarily placing males into an arena with three other males. The calling song structure of tactilely isolated males resulted in three factors: frequency (mean, minimum, and maximum frequencies); intensity (syllable intensity, and intensity difference); and variability (difference between syllable intensity and

frequency intensity). Males with high body intactness sang at lower frequencies. Asymmetrical males sang more intense songs. Large males sang with more intensity and frequency variability. Intermale competitions resulted in distinguishable linear dominance hierarchies. Lower-ranking males sang less often than higher-ranking males, altered singing times, and sang quieter songs. Intermale competition resulted in males altering song structure. Analysis of post-competitive songs resulted in three factors: frequency (mean and maximum frequencies, and intensity difference); energy (duty-cycle, intensity, and minimum frequency) and variability (unchanged). Higher-ranking asymmetrical males sang at lower frequencies. Higher-ranking males sang with greater energy, and timed their singing to female receptive times. Higher-ranking, large, intact males sang with less variability. This study indicated that *A. domesticus* males signal phenotypic information via their calling song characteristics. More specifically, in low population densities males signal information concerning their fitness-related qualities. After having established dominance orders, the male signal information concerning their rank in conjunction with fitness. The implications of this study were that

intermale competition altered the song cues available to the females and may alter female mating decisions.

"to win in battle over rivals....[and] to charm the females
(Darwin, 1871)

INTRODUCTION

Darwin's (1871) theory of sexual selection suggests that organisms can evolve through means of intraspecific mechanisms involving mating decisions and competitive interactions. In most species, females make the mating choices, and males compete for female affections. Sexual selection theory refers to these two processes as female choice and intermale competition. Acting independently, in concert, or in conflict, these two processes of sexual selection can result in evolved outcomes (physical or behavioral traits) that are either distinct, synonymous, or confounded (Alcock, 1989; Arnold, 1983; Borgia, 1979, 1981; Daly & Wilson, 1983; Ewing, 1984; Halliday, 1983; O'Donald, 1980, 1983; Thornhill & Alcock, 1983; Trivers, 1979). Determining whether the source of a mating decision is due to female choice or decided by intermale interactions has proven challenging. It is along these lines of inquiry that this study was undertaken. Most specifically it addressed the question, what male song cues signal male mate quality to a discriminative population of females? This paper reports the results of a study conducted to examine the morphological, behavioral, and environmental sources of variation in the

structure of the male cricket calling song as specified by sexual selection theory. These song structure variations may be important in attracting mates, fending off competitors, and ultimately influencing male reproductive success.

By way of introduction, the reader will first be presented to the field of cricket bioacoustics involving cricket calling song. Next, the implications of sexual selection and its relation to acoustic communication and cricket song will be reviewed. Furthermore, the implications as to the study of dominance relationships and their application to cricket social structures will be discussed. Finally, following a brief review and critique of the research literature on this topic, the unique goals and hypotheses generated by this study will be discussed.

Cricket Acoustic Communication And Life History Of Acheta Domesticus

Crickets are best characterized by their distinctive nocturnal species-specific calling songs (Alexander, 1961; Bennet-Clark, 1989; Cade, 1979; Ewing, 1989, Huber, 1962; Pierce, 1948; and others). Even untrained human observers can identify song differences among the various singing cricket species. Acoustic signaling is a risky business that costs energy, limits time spent feeding, and potentially leads to predation and parasitism; such that the general

broadcasting of acoustic signals (e.g., calling song) is more characteristic of male adaptations than female (Cade, 1979; Ewing, 1989; Walker & Masaki, 1989). Female communicative adaptations are usually limited to less general signaling systems and rely more on species-exclusive signaling mechanisms, such as pheromones (Bailey, 1991).

Any advertisement display, such as male cricket calling song, raises two categories of questions (Ewing, 1989): (1) what is the specific function of the behavior, and (2) what mechanisms underlie achieving those functions? Research evidence indicates that the primary function of calling song is to mediate encounters between sexually receptive conspecific females and the calling males (Alexander, 1975; Cade, 1979). The evidence verifying this role of male calling song is overwhelming. Copulatory unions and mating decisions are contingent on the female being attracted to male calling song. Female crickets make initial mating decisions based solely on the information conveyed through male calling song; being attracted to males of their species, and locating them through sound properties indicating the male's location (Huber, 1955). Furthermore, females may attend to calling song variations conveying information regarding the males' phenotypic attributes (e.g., for purposes of optimizing fitness-related traits or assortative mating, etc.) (Bailey, 1985, 1991; Bailey, Cunningham, & Lebel, 1990; Crankshaw, 1979; Forrest, 1983; Forrest & Green,

1991; Forrest & Raspet, 1994; Gwynne, 1981, 1982; Hedrick, 1986, 1988; Latimer & Sippel, 1987; Simmons, 1986, 1988a). Moreover, females may not be the only intended recipients of calling song, males may also be targeted, and may respond to another male's calling (Alexander, 1961; Bailey, 1991; Ewing, 1989). Male responses to calling song may involve aggressive attacks, agonistic interactions, spacing behavior, song interference, and song attraction. These male responses to calling song appear to be indicative of its "competitive" functions. Evidence, indeed has shown that calling song functions competitively in signaling information concerning male spacing, territory maintenance, dominance relationships, and aggregation formation (Alexander, 1961; Cade, 1979; Ewing, 1989). All of these social competitive functions are in some way being communicated via the calling song features; and only after recipient females and males have made their initial responses to the calling song can visual and tactile assessments be made of the calling male.

Cricket calling song is produced by stridulation: the rubbing of one body part against another (Wilson, 1975). The stridulatory mechanisms of male crickets are located on the tegmina (nonflight forewings), and consist of a hardened chitinous scraper on one tegminum and a file lined with stridulatory teeth on another tegminum. During calling, the tegmina are raised at about a 45° angle, and sound is produced by rubbing the scaper against the teeth on the file

during the closing of the tegmina. The species-specific frequency is determined by the number of teeth struck during stridulation (Bailey, 1991). In most species, not all the file teeth are used to produce the species-specific frequency during calling (Pierce, 1948). This allows for frequency modulation by the cricket which can alter the number of teeth struck, resulting in song characteristics changes and production of other types of songs. In addition to the file and scrapper, two other features on the tegmina are important to calling song: the harp and resonator areas. These two areas enhance the frequency and the projection of the calling song. The harp area is the primary radiator of the song frequency, while the resonator area affects the overall power output of the sound produced (Michelsen & Nock, 1974). In addition, the small sound-producing apparatuses such as the cricket singing assemblies are more consistent at producing higher frequencies (Bailey, 1985). Lower frequencies have longer wavelengths, and at some point (if lower frequencies are selected for) the potential wavelength of the cricket's song could possibly become longer than its body, a physical impossibility without the help of resonance structures, such as harp areas on the wings, or fashioned burrows or baffles that resonate at lower frequencies (Bailey, 1991). A shift to higher frequencies is easier for the small-bodied cricket, as the courtship song indicates; for *A. domesticus* the calling

song is at about 4-5 kHz, while the courtship song is at about 9 kHz. Shifts to higher frequencies are common.

Calling song specifically functions at a distance to attract females and competitively signal to other males (Phillips & Konishi, 1973). At close range, males use specialized songs to further enhance attraction or aggression (Alexander, 1961). Tactile encounters with females result in the production of courtship song, a soft trill-like humming at frequencies substantially higher than that of the calling song (Alexander, 1961; Pierce, 1948). Tactile encounters between males result in aggressive song, also called rivalry song. Rivalry song is acoustically differentiated from calling song by its temporal structure and frequency components (Alexander, 1961). While these specialized songs may be important to male reproductive success, the goal of this study was to isolate acoustic information conveyed by males prior to visual and tactile inspection. This study was conducted exclusively on male calling song, however, it was important to distinguish these songs from calling song and to characterize the labile nature of sound production in crickets.

The house cricket, *Acheta domesticus* (Orthoptera: Gryllidae), is a mostly gregarious, micropterous cricket native to Europe. It is also reared for commercial purposes on cricket farms in North America, probably due to its more gregarious nature than native North American species (Walker

& Masaki, 1989). House crickets are found in aggregations and rarely make burrows or defend territories. This gregarious quality makes them far less aggressive than most other field crickets (Alexander, 1961). House crickets live in what appears to be a single "lekking" area with social structures described as hierarchical dominance orders (Crankshaw, 1979). To date, however, the hierarchical nature of these dominance orders have not been fully characterized.

House cricket males do not provide any nutritive resources to the females. Male house cricket spermatophores merely provide sperm and a copulatory plug which the female pulls out after copulation. The resource investment in the male spermatophore is small, and studies in a closely-related species, *Gryllus bimaculatus*, indicate spermatophore sizes of only about 0.18 percent of the male's body weight (Simmons, 1988a). Spermatophore measures on *A. domesticus* were not readily available in the literature.

The calling song of *A. domesticus* has a simple structure consisting of distinct chirps of usually three syllables which are produced at a carrier frequency of about 4-5 kHz (Stout, DeHaan, & McGhee, 1983). These chirps are produced at fairly irregular intervals, such that chirp repetition rate is highly variable (Alexander, 1961; Stout et al., 1983). *A. domesticus* rivalry song, produced during aggressive encounters, is characterized by rapidly produced chirps (i. e. has a shorter chirp repetition rate) and a

higher fundamental frequency (Alexander, 1961). A. *domesticus* courtship song, produced during sexual encounters, is characterized by a soft-trilled humming produced at about 9 kHz (Pierce, 1948) and is accompanied by male body gyrations.

Sexual Selection Theory

Darwin (1859) distinguished two types of selection: natural and sexual. Natural selection is characterized by the differential ability of varying genotypes to survive in the environments they encounter. The adaptive traits of a species are shaped by the differential survival rates of these competing genotypes (Dawkins, 1982). Sexual selection is characterized by the differential ability of varying genotypes to acquire mates. Genotypic change caused by sexual selection results from two intraspecific interactions: (1) the competitive interactions between members of the same sex to acquire mates--intrasexual selection, and (2) the intersexual mating decisions based on phenotypes the choosier sex finds attractive--epigamic selection (Darwin, 1871; Maynard Smith, 1978). These two processes of sexual selection: intrasexual and epigamic selection are commonly referred to as intermale competition and female choice, respectively (Fisher, 1930). As recognized by Darwin (1871), it is commonly the males that compete for access to females,

and the females that choose among the males for the most attractive mate. Trivers (1972) extended the idea of sexual selection to include the outcomes of differential parental investment. Males, because they invest less in offspring, usually only sperm, can increase their reproductive output by increasing the number of mating opportunities. Males can have substantially more offspring than females because they do not have to directly contribute resource investment into the offspring. As a result, male reproductive output is more variable than female reproductive output (Bateman, 1948). Some males may mate with several females and some males may never mate. Females invest substantially more into their offspring and usually breed at their reproductive capacity (Daly & Wilson, 1983). More fertilizations do not increase female reproductive output, which is limited by other factors which influence egg production, such as food availability. In this way, the reproductive variance among females is substantially less than among males. Based on these effects of differential parent investment, males more often compete among themselves for access to females, and females choose more carefully among prospective mates.

Traits evolved through these sexual mechanisms were selected for by how well individuals with different genotypes were able to reproduce. Genetic survival means producing offspring. An inability to reproduce means that an organism's genes die with it, no matter its survival

capabilities (Dawkins, 1982). Due to this aspect of genetic survival, sexual selection often conflicts with natural selection as to what phenotypic traits evolve (Bateson, 1983; Darwin, 1871). Darwin was astutely aware that activities and traits necessary to acquire a mate were often detrimental to individual survival. Certain traits, such as bright coloration, large morphological weaponry, and conspicuous signaling, use precious energy reserves (Hutchinson, McNamara, & Cuthill, 1993; Zahavi, 1975; Zuk, 1984) and increase predation and parasitism (Burk, 1988; Ewing, 1989). However, in order to persist in time, a genotype must be competitive in the reproductive arena of selection.

Although cricket song evolution can be explained in general by natural selection, song presumably evolving because it enhanced the fitness of singers relative to nonsingers and being mutually beneficial to males and females (Ewing, 1989), the variant strategies of the two sexes may very well have had an impact. Cricket song may have been shaped by the females, in choosing among different song characteristics in males, or by males through competitively controlling what other males can sing. Both female choice and male competition together may have shaped male singing behavior and song characteristics.

Because females make such high parental investments in their offspring, it is important for the females to make wise decisions regarding the genotypic fitness of their offspring.

Choosy females may potentially make mate selections based on (1) the quality of the males' genes (Grafen, 1990; Parker, 1983; Wilson, 1975; Zahavi, 1975, 1991; Zuk, 1984), (2) whether or not the males can offset her investment costs through resource "gifts" (Eberhard, 1985; O'Donald, 1980; Thornhill & Alcock, 1983), or (3) through the simple attractiveness of a male trait to a discriminatory female population (Fisher, 1930).

Theories suggesting that females select males based on the quality of their genes are called "good genes" theories (for reviews see Arnold, 1983; O'Donald, 1983). The primary assumption of "good genes" theories is that there is heritable genetic variation for fitness; however, these fitness components are hidden, such that male phenotypic traits are only secondary indicators of these underlying genetic fitness components (Arnold, 1983). These theories suggest that the ostentatious phenotypic traits of males such as ornamentation and acoustic signaling evolved because they provided cues to females as to the underlying fitness of the males. The implication is that females which select males based on phenotypic traits that indicate an underlying "quality" genotypes will confer fitness advantages to their offspring (Gould & Gould, 1989). Choosy females avoid suboptimal genes in their offspring by assessing and selecting morphological and behavioral phenotypic indicators of genotypes that promote good health, physical prowess,

dominance, and pathogen and parasite resistance (Daly & Wilson, 1983; Grafen, 1990; Møller, 1993b; O'Donald, 1983; Parsons, 1990; Thornhill, 1993). Partridge's (1980) study of female fruit flies provided evidence for this by demonstrating that females allowed to choose their own mates from a variety of males had fitter offspring (in terms of survival and reproductive outcomes) than females provided a single male.

There are two prominent hypotheses regarding how "good genes" are phenotypically encoded or indicated: (1) the handicap hypothesis and (2) the healthy-male hypothesis. The handicap hypothesis, proposed by Zahavi (1975) suggests that females pick males based on the severity of a detrimental "handicap." The ostentatious traits carried by males, such as ornamentation, are handicaps evolved to indicate other underlying fitness-related genotypic traits, such as health, strength, immune function, and so forth that allow the males to survive and promote the severity of their handicaps. Only males of good genetic quality are able to survive with the burdensome handicap. The more severe the handicap the more efficacious the indication of the male's genetic quality. Females that prefer bigger and brighter are, in effect, selecting the most fit males and passing on high fitness-related genes to their offspring. Two major criticisms against the handicap hypothesis are that (1) in genetic modeling, an invading "handicap gene" does not spread in a

population (Daly & Wilson, 1983); and (2) choosy females have male offspring that inherit the handicap, canceling any fitness gains. Daly and Wilson (1983, pp. 134) suggest that the proposed genetic models questioning the validity of the handicap hypothesis are not designed in the right spirit. The handicap, they say "is probably not best conceived of as an inevitable fitness penalty...[but] is expressed only in those individuals who can 'afford' it." In other words, many males are available for females to choose from, but only a few possess the handicap to the necessary degree or severity that females prefer it. In light of the second criticism, it is true that a female's male offspring may inherit the handicap, but her female offspring offset this cost by accruing the benefits without the handicap costs. This implies that handicaps are selected for based on the fitnesses of the female rather than the male offspring.

The healthy-male or parasite-resistance theory proposed by Zuk (1984) suggests a plausible complement to the handicap model. It proposes that sexual dimorphisms are energetically expensive to maintain, and lose their clarity or brightness if a male is not healthy (e.g., is subjected to starvation, pathogens or parasites) or has a weak immune system. Bright plumage or loud calls are signs of health, and indicate genes conferring pathogen and parasite resistance (Daly & Wilson, 1983). Females with preferences for indicators of health will provide those "healthy" or immune function genes to

their offspring. Bird studies have shown that females mating with mite-infested males have fewer hatchlings of low emergence weights and prone to mite-infestation (Daly & Wilson, 1983). Parsons (1990) has proposed that a reliable phenotypic indicator for strong immune function is body symmetry. According to Thornhill (1993), pathogen attacks during development can result in morphological asymmetries; individuals with strong immune systems avoid these developmental difficulties and are more symmetrical.

In addition to suggesting why males carry costly handicaps or engage in costly behaviors, "good genes" theories suggest that the costs of these traits cause them to be honest advertisements of fitness related genotypes. These "good genes" traits or handicaps are self-evident, and cannot be counterfeited (e.g., size, health, dominance) effectively because they require male genetic robustness to adequately achieve. The fitness benefits to females that are discriminative along these traits would favor a choosy female population, which in turn enhances "honest" advertisement of genotypic quality in males. In fact, sexual selection based on these fitness advantages has driven females to evolve behavioral mechanisms that allow them to discriminate between males of varying genetic quality. Furthermore, phenotypic traits that could be feigned by the males were ignored by females and declined in the male population (Hutchinson et al., 1993). Female choice must have regularly driven the

selection for male traits that are "handicaps" or indicators of health (Zahavi, 1975, 1977; Zuk, 1984). Female choice, in turn, promotes the male display of traits that honestly advertise their genetic and phenotypic quality (Daly & Wilson, 1983; Zahavi, 1975, 1977), such that the good genes theories generate evolutionarily stable strategies of honest signaling (Grafen, 1990). In other words, the best strategy is to signal phenotypic traits honestly, since dishonest signaling is, first, unobtainable by males without the fitness to absorb the costs and, second, is ignored by females. Grafen (1990) further establishes the notion that biological signals are indeed substantial handicaps to signalers. Cricket calling may be classified as a handicap and indicative of male cricket fitness, since only highly fit males are able invest the time and energy into singing. As Hutchinson et al. (1993) clearly notes "song is...an honest signal only because it is expensive."

Critics of these "good genes" theories argue that selection based on female preferences for heritable fitness would eventually cause fixation of the highest fitness traits in all males in the population. The end result being that variation in fitness of the trait (such as a handicap) would reach genetic equilibrium (Maynard Smith, 1978). If this genetic equilibrium occurred then female preferences were of no value because all males possess the optimal genes. Borgia (1979) has contended that most models whereby genetic

equilibrium was achieved were based on simplified additive genetic models. Nonadditive genetic models result in different conclusions in regards to reaching a genetic equilibrium. Borgia also suggests that the level of heterozygosity affects the fitness of offspring: higher levels of heterozygosity are linked to increased fitness, a phenomenon known as hybrid vigor. Levels of heterozygosity are always in flux, such that the goal of a choosy female may be maximizing levels of heterozygosity in her offspring. Moreover, the healthy-male hypothesis is based on pathogen and parasite resistance. This system is driven by host-parasite coevolution which can prevent "good genes" from going to fixation because the same genes are not always the best (Thornhill, 1993).

In addition to these "good genes" theories, one other female choice theory that explains conspicuous male displays is runaway selection theory proposed by R. Fisher (1930). According to Fisher, the evolution for exaggerated traits in males could occur simply if females preferred them. Fisher hypothesized that any male trait preferred by a choosy female population would result in "runaway selection": the male trait becoming ever increasingly exaggerated until survival limitations brings it to a screeching halt. The underlying implication is that detrimental male traits arose because females found exaggerated traits appealing. Although runaway sexual selection is another plausible mechanism of female

choice, it yields no systematic predictions regarding male phenotypic traits females will prefer. Therefore, it does not provide an adequate theoretical foundation for this study.

The second process of sexual selection is intrasexual competition, usually by males. Intermale competition is, as its name implies, the struggle between males for possession of females (Darwin, 1871). As discussed previously, males usually invest substantially less in parental care than do females (Trivers, 1979). This makes females and their gametes a highly-valued commodity to males; a commodity worth fighting for, even to the death (Maynard Smith, 1978). Since the primary concern of each individual male is the enhancement of his reproductive success, the limiting factor for the males is the number of successful matings they acquire (Daly, 1978; Darwin, 1871; Maynard Smith, 1978). Thus, males become competitors and rivals to each other as they attempt to acquire matings. With sperm as their only major reproductive cost, males of most species with low parental investment attempt to acquire as many females as possible in order to maximize their reproductive gain in terms of matings resulting in offspring (Wade & Arnold, 1980). The more matings one male can monopolize interferes with other males chances to mate. As Bateman's principle implies, the variability in male reproductive success is greater than among females because of the competitive

interference of other males. This results in competition: conflicts over access to females, whether that be outracing other males, monopolizing females or resource sites, or controlling the signaling potential of other males. Adaptations evolved through male competition are those physical and behavioral attributes that confer some advantage to an individual male over rival males (Darwin, 1871; Maynard Smith, 1978; Wilson, 1975). Intermale competition results in strategies employed by males to acquire the most and best mates.

Males must accomplish two goals in the sexual arena (Darwin, 1871): (1) entice females to mate with them, and (2) fend off other males. These two struggles result in distinguishable phenotypic adaptations and behavioral strategies that allow the males to effectively compete (West-Eberhard, 1983). Competition results in a mating system among males that is best characterized as polygamy. Male reproductive success when male parental investment is low is maximized by polygamy, because the males can sire more offspring with more females. When male parental investment is high, the benefits to being polygamous are reduced, since the males can only give so many resources. Female reproductive output is not contingent on the number of fertilizations she acquires, but rather on the number of eggs she can produce. Most females obtain enough sperm in a single mating to fertilize all her eggs; for this reason

females of most species are less polygamous, usually mating with only one or a few males. A polygynous mating system is based on males acquiring matings with several females. The major limitation to a male acquiring multiple matings is his ability to best rival males. Therefore, several strategies are employed by males to achieve polygyny, most of which are based on competition.

The competitive tactics males employ to achieve polygyny depends on the degree to which males can monopolize the female population. Competitive strategies that will be productive to the males depend on (1) the behavioral ecology directing female behavior (i.e. the degree to which females clump or disperse), and (2) female distribution in the environment (Alcock, 1989). Basically, male competitive strategies are based upon where females can be found; and result in two categories of competitive strategies: scramble competition and contest competition. Scramble competition is essentially a race between males to be the first to find a female and mate with her. Scramble competition among males occurs when females are widely distributed throughout their environment or when the costs of monopolizing several females is too expensive; such a situation occurs when there is a large numbers of competitors which make defensive of females impossible. Scramble competition results in a searching fervor by the males and any combative competitive usually revolves around the vicinity of a female. In most scramble

competitive species, the males ignore each other since their ultimate objective is finding females and not fighting among themselves. Strength and speed usually win the race. The male phenotypic traits that arise are based on strength, endurance, and travel and searching abilities. The winners in scramble competition are those males that are the most persistent, durable, and perceptive searchers (Alcock, 1989; Thornhill & Alcock, 1983; Wilson, 1975).

If, however, females are somehow clumped in their environment, by being gregarious or by collecting at resource sites, such that the males do not have to scramble to find widely distributed females; males can achieve substantial mating opportunities by involving themselves in defense of the females or the resources. This situation results in the second category of male competitive strategies: contest competition. Since the female distribution is monopolizable, males gain by direct competition with each other to monopolize the females (Alcock, 1983; Gould & Gould, 1989; Thornhill & Alcock, 1983; Wilson, 1975). In other words, there is something to be contested. Contest competition results in fierce struggles between the males for control over the female group or areas containing the resources. Depending on the ecological factors that cause a clumped female distribution, males will adopt different strategies for monopolizing the female population. If the females clump together socially; for example, female ungulates herd

together as a means of predator defense, then the males can monopolize and defend the female group. This type of contest strategy is called female defense polygyny (Alcock, 1983). Since the group of females may move from area to area, the males' best strategy is to control sexual access to the group of females as they move about. In contrast, if the female population is clumped together due to a limited resource, whether it be food, water, egg-laying sites, and so on, then the males can defend the area containing the valued resource, and copulate with females as they enter the area to obtain the resource. This type of contest strategy is called territory defense polygyny, since the territory containing the resource is such that it can be defended and the females using the resource can be monopolized (Alcock, 1983). The most cost effective strategy for males is to patrol and expel rivals out of the territory. Territorial defense must involve a particular site of value to females such that a male's chance of encountering several females is high. Defense of the site will allow the male access to the females coming for the resource.

A territorial strategy is contingent on the value of the site. Most territorial mating strategies involve valued resources such as food, water, and egg-laying sites where the females congregate; however, in some species the males defend territories that seemingly have no valued resources. Instead the site's apparent value is the males themselves.

Territories such as these are called display territories. These display territories are sites where numbers of males converge for the purpose of displaying to receptive females. Females congregate at display territories in order to obtain matings. Interestingly, this type of male strategy occurs in species where females are not very monopolizable, and is related to scramble competition. The apparent cause for the female insects seeking out males is probably related to the longevity of the females of the species: short-lived females may be under strong pressure to mate quickly (Thornhill & Alcock, 1983). Often male display territories are near prominent landmarks such as elevated peaks or open fields. There are two types of display territorial strategies: defense of individual display sites and group defense of a single "lekking" display site. Calling sites in field crickets (in general) provide a illustrative example of a species that use an individual display territory strategy. Field crickets usually call from open fields and meadows; usually bordered by denser wooded areas around them. These sites in the field cricket's environment are preferred for calling, because they are prominent and allow for greater song power and radiation. Additionally, when calling is done *en masse* (males taking up calling sites nearby one another), the power output increases, which is more attractive to females (Alexander, 1975; Cade, 1979). These calling behaviors cause males to congregate in an single area, taking

up individual display territories nearby other calling males, for the purpose of jointly attracting females. Females come out from foraging in the denser foliage to select a mate or mates from the calling males. Once the females enter the area, they can move about the group of singing males, before choosing to copulate. In this way, females can sample among the calling males as demonstrated by Feaver (1983) in katydids, and by Latimer and Sippel (1987) in bushcrickets. Display territories have no resource to females other than the males. Individual display sites consist of small "copulatory" areas defended by the males. Within this copulatory area, a male can monopolize all the females he attracts to his area without interference from other males. Field crickets again provide example as described by Alexander (1961) and Cade (1979). Male field crickets usually dig burrows into the ground and defend the area around the burrow. This is also his calling site. Fights over burrows and calling sites can be intense as attested by Alexander (1961) who observed one disorientated male fighting the resident male over a burrow perceived as his. The fighting lasted for hours. Within these individual display areas, the male monopolizes any female attracted to his area. This contrasts from the group "lekking" sites of more gregarious species, where all males occupy one large display territory. Within these lekking areas, there is no safe "copulatory" areas defended by the individual males, rather

the males contend for the "right" to access of any females entering the lekking area. Competition within the "lekking" group for various levels of access results in a hierarchy of levels, some males achieving first priority access, other males second priority access and so on. The level of "right" [to access of females] a male achieves has thus been termed his dominance status. Most observed structures resulting from competition for various levels of right have been identified as hierarchical and subsequently called dominance hierarchies (Wilson, 1975). Derived from this dominance concept, this type of strategy is also known as male dominance polygyny (Thornhill & Alcock, 1983). Dominance position and mating success have been linked together in such diverse species as crickets (Alexander, 1961), elephant seals (McCann, 1981), and baboons (Haustater, 1975)

By comparison with scramble competition, contest competition results in traits that allow the males to compete successfully for the contested resource. Whereas mice who race around to find females are built for speed and endurance (male mice are small and sleek); the males of herding species, such as sheep and elk, have cumbersome and weighty horns and antlers that limit speed and endurance, but are very effective weapons to repel rival males from their harems of females. In territorial species, males have attributes that allow them to expel competitors from their territory. Behavioral attributes such as tenacity to defend a territory,

even to the death, are beneficial since territorial males rarely lose (Alexander, 1961). However, in a "lekking" species, such as the house crickets of this study or in social species, such as baboons where territorial areas are shared, fighting to the death may not be so beneficial and behavioral adaptations that allow for submission will arise (to be further discussed in the section on intermale competition and acoustic signaling). Based on these considerations of male competitive strategies, males achieve reproductive success by acquiring strategies and physical attributes that allow them to effectively obtain polygyny based on female socioecological constraints and rival males' competitive strategies. Males have evolved specialized anatomical adaptations that allow them to compete against other males, such as weaponry (e.g., horns, size), ornamentation, sperm displacement apparatus, and specialized behavioral adaptations (competitive strategies).

Males seem to be more susceptible to the elaborate and excessive traits produced by sexual selection, whereas females seem to be more characteristic of what natural selection would have formulated (Darwin, 1871). This trend seems to be the most pervasive in the biotic world, although competition is not exclusive to males and choice is not exclusive to females. For example, in Mormon crickets the males' spermatophores are so valuable that the males are choosy about what female they will mate with (Gwynne, 1984,

1988). As describe above, sexually dimorphic traits may have been shaped by female choice processes and intermale competitive. Male competition has been the most widely studied aspect of sexual selection, since its adaptive morphological and behavioral aspects are obvious and readily accessible to measurement. In the past, most studies focused on the effects of male competition or female choice for resources that the males had already secured as part of their competitive episodes. The major reason female choice was so neglected historically is that researchers treated female choice and male competition as mutually exclusive. If a role for male competition was determined then that negated the role of female choice. But, as we will discuss, for the most part most systems are mixed.

Female Choice And Its Relation To Acoustic Signaling

In many species the primary method by which females select mates is accomplished through direct observation of the males' physical attributes through a visual or tactile inspection process. This selection process makes it more difficult for researchers to isolate the phenotypic components of sexual advertisement from other irrelevant physical characteristics of the male (Huber, 1978). As discussed previously, male crickets use acoustic signals that attract females over long distances, usually many meters

away. These distances do not allow the searching female crickets access to visual or tactile contact with the signaling males before a decision to or not to follow the signal is made. This means that female crickets must make energy-consuming, predation-risky decisions before any proximate evaluation of potential mates can be made. Therefore, it is logical to theorize that the long distance acoustic signals of male crickets serve to attract potential mates by advertising the fitness related genetic quality of the calling male. A rational assumption is that since substantial genetic material is invested in a long distance calling system, it should also serve as a female choice advertisement system as well, in order to conserve genetic material.

Due to their large investment (energy expenditure and predation costs), evolution would drive female crickets to attend to signal characteristics that communicate information about the fitness related qualities of the calling males. Females that could discriminate what song deviations are correlated with certain fitness related characteristics would cut their costs and risks in finding quality mates. Discriminating females would have a two-fold advantage over nondiscriminating females: (1) they do not incur the costs of searching for and finding unsuitable mates, and (2) their offspring gain the fitness benefits of their high quality sires. Selection would have promoted females that could

discriminate between male crickets based solely on calling song indicators of fitness because this mechanism would afford discriminating females this two-fold advantage. Genes that allowed females to be discriminatory would increase in the female population. Moreover, males would be selected to advertise fitness related quality via song characteristics. Males that best advertised their fitness related quality through song characteristics would achieve greater mating success, due to their greater attractiveness to the discriminating female population (Arnold, 1983). Genes that allowed males to better communicate their phenotypic quality through song features would increase in the male population. The evolutionary outcome for acoustically signaling crickets should be a population of discriminating females and advertising males.

There are two reasons that cricket calling song may serve as a male advertisement of female choice parameters: (1) males are selected to advertise fitness related quality via calling song (as discussed above) and (2) the energy costs of calling song ensure the "honest" advertisement of male fitness (Hutchinson et al., 1993; Zahavi, 1975, 1977). The energy costs of cricket song would limit the number of "cheater" males, who could attempt to communicate song characteristics of phenotypic fitness without having the corresponding phenotypic qualities. The high energy expense required by the male house crickets (*A. domesticus*) for

acoustic signaling (Prestwich & Walker, 1981) make this an ideal system to investigate "honest" advertisement of male quality and female choice.

The female choice hypothesis specifies that: (1) females indeed discriminate among individual males within their own species, and (2) females discriminate among these males on the basis of the phenotypic indicators of male fitness (Eberhard, 1985; Thornhill & Alcock, 1983). Any demonstration of adaptive female choice between calling males based on characteristics of the calling song requires that the females respond preferentially to characteristics of the calling songs in the absence of males and, further, that these characteristics are correlated in some way with the male's mating success, since males would not evolve to communication features that did not enhance mating success (Searcy & Andersson, 1986).

Theoretically, certain components of a male cricket's calling song will: (1) communicate differential male fitness and (2) vary intraspecifically among crickets of different fitnesses. The females should, therefore, be sexually selected to form preferences around the song components that indicate fitness related quality. Cade (1979, pp. 371) states that "if female crickets are able to choose mates on the basis of differential male fitness, then such a preference probably depends on individual variations in calling song." Male advertisement will be contained in

physiological and mechanical traits that limit or enhance a male's singing potential so that song characteristics would vary along these traits. It follows that certain components of calling song function for species-specificity, and other components function as individual advertisement (Lloyd, 1981). Popov and Shuvalov (1977) suggest that the attractiveness of male song to a female results from the evaluation of all of the relevant components of the calling song. These relevant components of calling song fall into two categories: (1) "essential recognition parameters," features that identify the species, such as chirping vs. trilling and syllable number, and (2) "motivational parameters," features that make the song attractive to females, such as intensity and chirp rate.

Thornhill and Alcock (1983) suggest that properties of the males' sound production that vary in the vigor with which they are performed are probable cues to females about male individual fitness. Calling involves substantial energy costs. (1) Calling requires high metabolic costs, especially in terms of the intensity of the calling song. Males crickets of several species have evolved behavioral adaptations that enhance the intensity of their calls, while not increasing the energy costs (Bailey, 1991; Cade, 1979). These males cut costs by singing from burrows, perched on rocks, cutting leaves to act as baffles, and engaging in many other behavioral schemes to increase intensity without the

cost. These behavioral adaptations attest to the energy expense of calling. (2) Calling uses up foraging time. Low-quality males risk starvation if they sing (Hutchinson et al., 1993). Only males of substantial fitness can "afford" calling time. (3) Calling involves substantial risk. Calling attracts male competitors, predators, and parasites. Calling house cricket males are a primary prey of the female digger wasp, *Liris niger*, who locate their prey by their calling song (Gnatzy & Hustert, 1989). In addition, intermale competition can be severe and result in low survivorship for those males that cannot risk the energy use or the physical damage (Bailey, 1991). The energy costs of cricket song would limit the number of "cheater" males, who could attempt to communicate song characteristics of quality without having the corresponding phenotypic qualities.

Several female preferences (called "female choice parameters") for male phenotypic characteristics have been evaluated in crickets and related insect species. Male size has been the most studied phenotypic trait in mate choice studies, probably due to its ease of measurement and manipulation. It is theorized that large male size is preferred by females due to increased sperm production (females can mate fewer times) (Simmons, 1988b), indication of disease resistance (Thornhill, 1993), and protection afforded to the female, during and after copulation (Bailey, 1991; Thornhill & Alcock, 1983). A number of studies have

demonstrated female preference for larger males (in flies, *Scatophaga stercoraria*, Borgia, 1981; in katydids, *Conocephalus nigropleurum*, Gwynne, 1982; in field crickets, *G. bimaculatus*, Simmons, 1988b; Thornhill & Alcock, 1983). Large male size has been shown to correspond to a lower carrier frequency, since the sound-producing structures of the larger males are larger (Bailey, 1991). However, female crickets have better auditory acuity to high frequencies, and in the bush cricket, *Requena verticalia*, females show a preference for high frequency components in the males' calling songs (Bailey & Yeoh, 1988). In addition, larger males have been demonstrated to produce louder (more intense) calling songs (Bailey, 1991; Simmons, 1988a). Several studies have shown that females crickets prefer louder songs (in bush crickets, Bailey & Yeoh, 1988; in mole crickets, Forrest, 1983; Forrest & Green, 1991; Simmons, 1988a). Bailey (1985) has argued that the carrier frequency is probably the most reliable indicator of male size, since a song's intensity can vary with posture and distance. The loudness of a song may possibly be an unreliable cue, as it decreases with distance and a female may simply go towards the closest male. The intensity of a call, also increase the likelihood of finding a male's location. Female selection based on intensity may simply be "passive" attraction for the most localizable song as discussed by Parker (1983). However, this possibility assumes that females track and mate

with the first calling male they encounter. The female choice hypothesis suggests that females increase their fitness by sampling and selecting from a number a potential mates, as has been demonstrated by Partridge (1980). In addition to intensity, Simmons (1988a) has shown that the repetition rate of chirps and syllables were positively correlated to male size in field crickets.

Age may prove to be a "true" indicator of genetic fitness, since older males have demonstrated their ability to survive the rigors of selection (Halliday, 1983). Female field crickets (*G. veletis*, *G. pennsylvanicus*, & *G. bimaculatus*) have been shown to preferentially mate with older males (Simmons & Zuk, 1992; Zuk, 1987, 1988). However, no study has yet revealed any song structures corresponding to age (Ciceran, Murray, & Rowel, 1994; Simmons, 1995). Ciceran et al. (1994) suggest that even finer resolutions of song structure may be necessary. Recent studies in insects have revealed that the symmetry of male morphological structures indicates genetic fitness and immune function (Thornhill, 1992, 1993). Symmetrical individuals show greater ability to cope with stress (Parsons, 1990), overall higher fitness (Møller, 1993a), and greater ability to attract mates (Thornhill, 1992). Thornhill (1993) suggested that male size, nutritional status, and disease resistance would directly affect the frequency and intensity of male song.

Other aspects of male signaling behavior, duration of calling, (Cade, 1979, 1981) and calling-bout duration, (Hedrick, 1986), are known to be important to males for acquiring mates and may be correlated to physical characteristics as yet to be determined. Other avenues of research are pursuing the quantitative genetics of sound production as the underlying force of selection (Hedrick, 1988; Simmons & Roff, 1994; Webb & Roff, 1992). Little is known about the genetic variation of the calling song components in crickets. Several aspects of the sound production apparatus are probably subject to genetic variation, such as file-teeth number, file length, and the size and shape of the harp and resonator areas. Differences in these features may affect female choice in crickets (Webb & Roff, 1992). These possible genetic variations in the song apparatus may additionally be related to genetic variations in the male song components. As found by Hedrick (1988), the calling-bout duration of *G. integer* was significantly heritable ($h^2 = 0.75$), and females preferred males with longer bout durations. Webb & Roff (1992) found in *G. firmus* that all the morphological features of the males had significant heritabilities (for example; h^2 (file length) = 0.55 ± 0.21 ; h^2 (tooth number) = 0.42 ± 0.14); however, only one of the song components heritabilities was significant, intra-chirp pulse [syllable] rate ($h^2 = 0.35 \pm 0.17$). Few other song components have been investigated for inter-individual

variation between males that a female might discriminate and utilize.

In addition to the "pure" female choice parameters, the outcome of male competition may be vital to female choice. Male competition may reveal other male phenotypic attributes, such as pugnacity and "competitive skill," that may be important to the fitnesses of the female's offspring. Depending on the environment, in terms of population density, in which the females find themselves, their mate choice criteria and strategies may vary. Females in low density populations may opt to mate with males based purely on fitness related phenotypes and avoid males which have competitive tendencies. Competitive tendencies may not be beneficial in areas of low population density. These traits may be disruptive to courtship and copulation; and, therefore, hinder reproductive success of male offspring. In high density populations, competitive traits are important to the male's reproductive success. Females in high density populations may opt to mate with the most competitively successful males and pass these traits on to their male offspring. In this way, females may track population densities and alter their choice criteria to optimally select for traits that will be advantageous to their offspring in similar environments. The only time "competitive ability" or "aggressive motivation" in males can be determined is when the males compete. In order to evaluate the effects of

intermale competition on male calling song characteristics, the males in this study were permitted to interact and compete with other males.

Intermale Competition And Its Relation To Acoustic Signaling

In conjunction with their distinctive species-specific songs, crickets are best known for their aggressive behavior. The aggressive nature of male crickets in competition for territories and females has been well documented (Alexander, 1961; Darwin, 1871). In fact, cricket fighting has been popular sport in the Far East for at least a thousand years, due to the violent nature of the physical combats (Laufer, 1927). Many intense cricket fights end in injury or death to one or both of the combatants. Kato and Hayasaka (1958) were the first to characterize the outcome of this male aggressive behavior in crickets as a dominance order. Subsequent research by Alexander (1961) looked into the causes and structure of the final social outcome. In this study of field crickets, Alexander concluded that the primary social outcome for field crickets was the establishment of territorial display sites and, secondarily, when population densities were high, dominance hierarchies.

Male competitive social interactions have also been suggested to affect male calling song features and singing activity (Alexander, 1961; Cade, 1979; Ewing, 1989). Calling

song has multiple functions, many of which are competitive in nature. The competitive usage of calling song can involve interference with other males' calling (increasing intensity when other males are calling, Cade, 1979), maintenance of territorial boundaries (Alexander, 1961, 1975), and optimal distribution of males in a calling area (Ewing, 1989).

Suggested effects on the male's calling activities include modifications to the song parameters to competitively alert other males to the possession of a territory or acquired dominance status, or to cause interference with other males' songs. In order to attract sexually receptive females the males must call. Without calling song, a male cannot attract females. In crickets and other acoustically signaling species, being able to call is "access" to females and comparable to any other valued resource a male might compete for and defend. Any behavioral mechanism that allows one male to interfere with other males' singing activity or song output is advantageous. As in resource defense strategies, holding the resource confers reproductive advantages, and any trait that allows one male to dislodge another from the resource is selected for (Alcock, 1989). In the case of crickets, calling song is truly the "resource" necessary to acquire matings. Since singing ability is a presumed capacity of all males (barring developmental errors), behavioral adaptations to control and suppress calling in other males would be expected to have evolved. One potential

behavioral adaptation to serve this purpose, particularly in lekking species, would be the establishment of dominance relationships. As a behavioral control mechanism, establishing dominance relationships allows for differential access to females and other resources. One expected aspect of intermale competition, then, is competition for dominance status. Indeed, when several male crickets are confined together, they engage in frequent and intense physical fights (Alexander, 1961, Crankshaw, 1979).

A dominance hierarchy is said to emerge when individuals give way to more forceful opponents without the necessity for further fighting (Hinde, 1970). According to Hinde (1978) and Bernstein (1981), the concept of dominance is evoked when "asymmetric agonistic patterns" arise; which are imbalances in the behavioral responses between two individuals. The contestants in these bouts appear to "ascertain" which individual they can defeat and which can defeat them. At some point an important behavioral shift occurs when one individual acts to terminate the aggressive responses in another through submissive responses (such as fleeing). This submissive animal is, then, labeled the "loser" and the nonsubmissive animal as the "winner." If the loser persists in submitting to the winners aggressive behavior, then a dominance relationship is inferred to have developed between the two.

There are several questions to consider about the development of these dominance relationships. The first being "why do individuals engage in agonistic behaviors in the first place?" The answer to this question is simple, dominant individuals gain many reproductive advantages by establishing their dominance over other rivals. When superior competitors benefit by displacing weaker rivals and weaker individuals avoid harm by submitting to superiors, a dominance relationship will evolve (Bernstein, 1981; Hinde, 1978; Wilson, 1975; Wittenberger, 1981). The function of dominance is the acquiring of reproductive advantages, usually resources and females, by the dominants. Three main advantages to being dominant have been proposed, although many others may exist. (1) Dominant individuals have priority access to mates. Positive correlations between mating success and high status are the rule (Bernstein, 1976). (2) Dominant individuals have priority access to food, where survival is at stake (Bernstein, 1981; Wilson, 1975). And, (3) Dominant individuals have reduced stress (Wittenberger, 1981): dominants do not have to be concerned with aggression from submissives for access to food, to females, or being interfered with while copulating.

Despite advantages for being dominant, a corollary to the question of "Why compete for dominance?" is "Why accept subordination?" (Ewing, 1989). The primary answer to this questions is that subordinates avoid injury and harm that may

be inflicted on them by combat with larger, stronger, and more aggressive dominants. In addition, subordinates can choose at least three other options: disperse, submit, or adopt alternative reproductive strategies. In a territorial species, the best option for the losers is to emigrate and acquire a different territory, one that maybe empty or is defended by a weaker resident (Alexander, 1975; Cade, 1979). In situations where leaving is not an option, (e.g., there are limited resources, or where cooperative predator vigilance and defense are necessary for survival, or the species is social, and so forth), there is the option of being subordinate and adopting alternative strategies, such as being a *beta* male or satellite, to obtain matings. Examples of subordinate tactics include; primate subordinates attempting to sneak copulations, or in the case of some birds, subordinates becoming helpers to secure the succession of the territory to them in the next breeding season (examples cited in Daly & Wilson, 1983).

The concept of dominance relationships between nonhuman conspecifics is not a new concept. Dominance relationships were first introduced by Schjelderup-Ebbe (1922) describing them as pecking-order in domestic chickens. Since then the notion of dominance has acquired substantial support and criticism; and many ethologists have applied the term to explain the asymmetrical agonistic interactions between individuals of many species. However, dominance *per se* is

not a unitary concept and substantial debate has arisen as to the reality of its existence. The exigency for evoking the concept of dominance depends on its ability and utility to explain species-specific characteristics and behavioral interactions (Banks, 1981). The exact mechanism for acquiring or establishing dominance and the function of dominance varies as widely as there are numbers of species. Since much controversy surrounds the topic of dominance, it is worthwhile to present a more general discussion of dominance and how it influences the dynamics of intermale competition in crickets. For even more thorough discussions dealing with the concept of dominance, reviews by E. O. Wilson (1975) and Bernstein (1981) should be consulted. For this paper, a brief summary of the implications for measurement and assessment of dominance will suffice.

Anytime members of a species find themselves together, for whatever reason (e.g., limited space, resource sites), some sort of system of social organization must arise. Members of one's species are an individual's principal competitors encompassing more spheres of access, such as mates (Alexander, 1961, 1975; Bernstein, 1976; Dimond, 1984; Wittenberger, 1981). As individuals of a species come together, agonistic encounters arise, particularly in males (Darwin, 1871; Hinde, 1970). These encounters result in several potential outcomes: death, physical injury, status, priority access, or space between the two combatants.

Mechanisms that serve to lessen the severity of the encounter would be under strong selection. It may be argued that agonistic encounters need not occur at all; technically they do not have to, as in scramble competition where males ignore one another. However, if one individual can contest a resource and gain the advantage through aggression, there is probably a selective advantage. An unstable situation is created, one in which an aggressive genotype can invade a population (Maynard Smith, 1978; West-Eberhard, 1983). Such a situation could arise if an aggressive mutant arose in a population of passive individuals. At first, the mutant aggressors encounter all passive individuals, winning resources and reproductive success. Eventually the population becomes saturated with aggressors, such that aggressors meet other aggressors and disastrous fights ensue. At this point, passivity would be advantageous to survival, but still may not achieve sufficient matings to be reproductively competitive. Ultimately, the most stable strategy that would arise is one that involves submitting to aggressors who can defeat you, but not to those who can't: a dominance hierarchy of some kind. This strategy not only promotes survival, but it also secures matings. A final outcome of this nature clearly supports the contention that patterns of hierarchical dominance will evolve and be the most viable strategy.

Some argue that dominance is merely a human artifact forced upon animal behavior patterns by their human observers (Altman, 1981; Bernstein, 1981). They argue that dominance is a human construct imposed on animal behavior to facilitate human understanding; when in reality the concept bears no reflection on the behaviors involved (see Bernstein, 1981). The judgment as to whether this critique is valid or not ultimately rests upon whether the construct of dominance is a useful model for explaining the behavioral patterns actually observed in intermale aggression in nonhuman species (Banks, 1981). It seems inevitable, however, that competition in social interactions must of necessity result in some pattern of differential access (e.g., dominance). The controversies surrounding dominance lie more in the fact that its structure and function differs so radically from species to species, and human efforts to define and measure it are limited (Banks, 1981; Bernstein, 1981; Wittenberger, 1981). As Bernstein (1981) acknowledges, the outcomes of either evoking the notion of dominance or not are the same: the predictability of the outcomes of the agonistic encounters (the winner and the loser) between two individuals. In other words, does the behavioral construct, dominance, allow for prediction and explanation as to why one individual won and the other lost? Does the dominance construct define the behavior patterns between the two individuals, and predict the outcome? If dominance can account for and explain the

behavior patterns and the outcomes, then it must be an acceptable concept and useful for describing animal social interactions. One reason that it remains a distasteful concept to some researchers has more to do with dominance as a human phenomenon with its full connotations of the subjugation of humans of differing race and gender, and less to do with dominance as an organizing principle for patterns of behavioral interactions.

So, in summary, what is dominance? Dominance is a construct derived from the observation of aggressive and submissive behavior patterns between conspecifics. Dominance is a multi-faceted construct dependent on the species, sex, life history, and social context of the subjects involved. In terms of intermale competition, it accomplishes differential access to resources, spacing, territory, females, less interference during copulation, suppression of rival males, and probably more as yet unspecified outcomes. Careful attention to possible differences between species is necessary, since dominance behaviors may be of innate or learned origins (Banks, 1981). In Bernstein's (1981) critique, his perspective was one from the observation of complex primate species, where dominance relations are a multiple function of the other members of the group, involving generational overlaps, passing on status to offspring, and group coalitions. In crickets, the patterns of aggression and submission are simple and obvious

(Alexander, 1975). Reasons for this are as follows: (1) Crickets have a relatively short agonistic refractory period. An agonistic refractory period is the amount of time it takes for a cricket to recover aggressive tendencies after losing in an agonistic encounter. The dominance relationship requires periodic reinforcement, and frequent momentary reversals occur. Adamo and Hoy (1995) found that field crickets *G. bimaculatus* have about a 10 minute agonistic behavior refractory period. Male crickets were allowed to engage in aggressive interactions in dyads. After a defeat, the submissives were placed in isolated chambers for a specified amount of time (refractory period). Adamo and Hoy found that full agonistic expression of behavior resumed after 10 minutes of isolation, in other words, the male would behave as though no fight had been lost. Submissive males placed in a dyad before the 10 minute refractory period culminated would act submissively to any encounter with any male. This finding indicates that after about 10 minutes males resume full agonistic tendencies. In field crickets, this allows a male to lose to one male but then emigrate to another location and fight again. The refractory period for crickets (whether it be neurological or hormonal) appears to be about 10 minutes. In a hierarchical dominance group, this means that the dominance order has to be maintained by periodic reinforcement. (2) Dominance interactions are based on long term attributes of the individual males. These are

attributes such as pugnacity, strength, and health. As Alexander (1975) noted it does not appear that crickets are able to make individual recognitions, but that crickets maintaining tenacity and energy in an agonistic encounters win; for example, resident males defending a territory. Outcomes of cricket dominance encounters are clear-cut. (3) Cricket social organization is not complex. Cricket males stand alone so to speak, without help from coalitions or inherited dominance status as occurs in primates (Bernstein, 1981). Crickets do not form alliances with other crickets, or learn novel behaviors with which to terrify opponents. The agonistic behavior patterns of crickets are stereotyped and consistent. Wins or losses are based on the crickets morphological and behavioral attributes.

What role does dominance play in crickets? Agonistic encounters need not occur if male crickets maintain separate territories and only aggress when boundaries are encroached upon. This situation is characteristic of many field cricket species. Field cricket territories are established and maintained primary through the calling behavior of the resident males (Ewing, 1989). Field cricket males use calling song as a cue to residency and to maintain spacing. The intensity of the male's calling song determines how far away other males space themselves. These mechanisms minimize the occurrence of agonistic encounters. When passing through another male's territory, intruder males usually remain

silent (Cade, 1979). Studies looking at territory and spacing behavior in crickets demonstrate that certain aspects of male calling song function as competitive communication (West-Eberhard, 1989). Whether or not these intermale communicative cues are different from potential female choice cues is still unknown. If males ultimately signal dominance status (e.g., residency is equated to dominance position in many of these studies) in their calling song, it may be unnecessary to differentiate the song components for female choice from those of male competition, since female choice may reside on knowing which male is the better of the two in competition (e.g., the resident). It would, therefore, be a two-fold advantage for males to advertise their competitive status which simultaneously facilitates female mating decisions and warns other males. Latimer & Schatral (1987) have demonstrated in bushcrickets, *Tettigonia cantans*, that female choice cues are characteristic of dominant (resident) male calling song.

Mechanisms of intermale interactions and aggression are contingent on population density. This is why dominance hierarchies have been so criticized as an artifact of experimental confinement (Flannelly & Blanchard, 1981; Wittenberger, 1981). The criticism of these studies is that laboratory conditions limit dispersion in the male population, a characteristic response pattern in many territorial species. Therefore, the resulting dominance

hierarchies are an artifact of the laboratory setting. However, conditions in nature may occasionally cause high population densities, such as are found in the laboratory. These conditions warrant behavioral adaptations necessary to deal with high population and maintain male social organization. In low density populations, individual display territoriality in field crickets predominates (Alexander, 1961; Cade, 1979). The crickets maintain optimal spacing by distancing themselves by song intensities (Ewing, 1989), and by boundary defense (Alexander, 1961). However, when population densities intensify, sufficient spacing and dispersion are unattainable, and the males encroach on one another. These encroachments lead to intense fighting and aggressive behavior, and usually a dominance hierarchy results. In addition, Alexander (1961) found increased population density decreased the frequency of calling behavior. He attributed this to the increase in random encounters that the males had with females, an effect that, in turn, decreased the benefits to calling and territorial defense. Defense was too costly with so many competitors and too few territories for calling; such that both the costs to calling and the benefits to noncalling increase. Under such circumstances, the establishment of dominance hierarchies can maintain intermale social organization, and competitively determine which males continue to sing and which adopt nonsinging strategies.

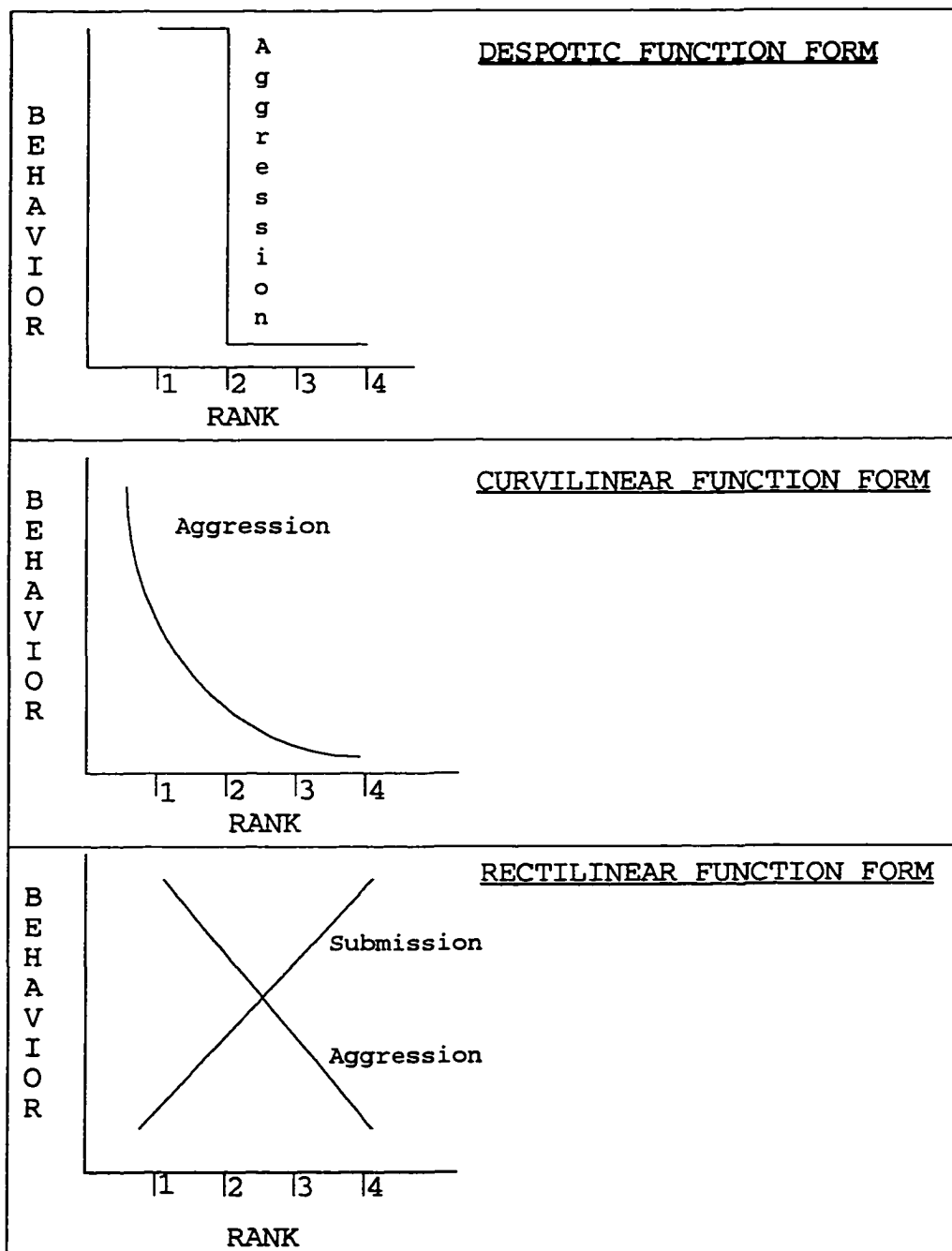
As discussed, field crickets (*Gryllus*) defend individual display sites. Field crickets demonstrate male spacing behavior and attachment to calling sites (Alexander, 1961). In low density populations, the outcomes of agonistic encounters between field crickets resulted, for the most part, in dispersal. However, even in field crickets (*G. integer*), Cade (1979) found that in spite of dense populations, a substantial portion of uncolonized areas remained uninhabited, suggesting possible indications for the establishment of dominance orders. Cade suggested that noncalling for some males has greater returns than dispersing, and acquiring new calling sites, in spite of the fact that noncalling males had relatively infrequent matings. In crickets, the territorial-dominant males almost always monopolize females, often searching for and attacking signaling males (Alexander, 1961; Crankshaw, 1979). The calling song of the resident (dominant) males consisted of regular, high intensity calling, which attracted females and interfered with calling in other males in areas around the resident. In response to the dominant, Cade (1979) identified four alternative behavior patterns in subordinate *G. integer*: two calling strategies, (1) irregular, low intensity calling and (2) calling at sunrise; and two noncalling strategies, (3) noncalling satellites and (4) noncaller attacks on the resident. The irregular, low intensity calling strategy attracted females without

eliciting attacks from other males, in particular nearby territory holders, and possibly functioned to avoid parasitism and steal incoming females. Calling at sunrise, may be a last resort effort by subordinates to attract females in the vicinity without eliciting attacks from nearby resident males. The noncalling strategies consisted of satellite behavior and attacks on calling males. Satellite males remained near calling males and intercepted incoming females, while at the same time avoided both parasitoids and male attacks. The noncalling attacker strategy is interesting, since the attackers usually loses any direct fights with the resident. Its function probably serves to interfere with copulation and possibly dislodge a female from the resident.

House crickets (*A. domesticus*) are for the most part group lekking and not highly territorial. House crickets form dominance hierarchies as reported by Crankshaw (1979). The house cricket provides an opportunity to investigate cricket agonistic behavior patterns in terms of dominance ranks and hierarchies, and in determining what male attributes affect dominance status and if such information is signaled in calling song. First of all, the structure of the dominance organization as it pertains to determining the meaning of rank can take many forms. As discussed by Bernstein (1981) and Wilson (1975), dominance organizations can be complex. This discussion will be limited to forms of

transitive, hierarchical organizations, due to the fact that cricket social organization is of limited complexity--nonhierarchical structures are not presumed to persist.

Hierarchical dominance structures can have varying degrees of dominance control as defined by the agonistic behavior patterns. Wilson (1975) has suggested two patterns of hierarchical dominance structures: despotism and linear hierarchies. It is probably easiest to think of the different types of dominance structures in terms of their measurement scales, after all they are based on the mathematics of these scales as applied to the cricket behavior patterns. Despotism is based on a nominal scale. The dominant position is the only meaningful rank in terms of explaining the behavior patterns (see Figure 1). One male assumes full dominance of the group space, so to speak, and all the others are equally subordinate. The agonistic behavioral patterns representing a despotic structure involve the 'dominant', male aggressing and all others submitting. The relationship between the nondominants (subordinates) involves no behavioral imbalances; all are 'losers.' In other words, only one rank is definitive, that of the dominant (despot). Despotism is the simplest mathematical structure of hierarchical dominance. One male assumes control of the space provided and all the others are equally subordinate, lacking asymmetric agonistic behavior patterns among themselves. If asymmetric agonistic behavior patterns

Figure 1: Patterns of Dominance Structure

(i.e., dominance relationships) exist between the subordinates, (i.e., patterns of unequal aggression and submission), then the importance or the meaningfulness of these ranks becomes relevant for explaining the behavior patterns and outcomes.

These types of hierarchical formations have been characterized in the literature in terms of linearity (in term of actual social ordering, not transitivity), where they are called linear hierarchies. Linearity in this sense, however, is a deceptive term that implies an interval structure for data that usually are only ordinal. Behavioral outcomes are ranked in a relative order, but not based on equivalent rates of aggression and submission (see Figure 1). In an ordinal sense, there are behavioral asymmetries in terms of aggression and submission between each rank in the order, but these asymmetries are not equivalent. A uniformly linear order such as rectilinear hierarchies involves the greatest degree of social complexity (in terms of linear orders). A rectilinear dominance structure explains agonistic behavior patterns and outcomes in terms of an interval scale: the dominance outcomes are ranked based on equivalent rates of behavioral occurrences (see Figure 1). The dominance ranks are meaningful in that they indicate equivalent behavior differences between the crickets. For instance, a simple pattern of rectilinear aggression would be Rank 1 aggressing twice against Rank 2, four times against

Rank 3 and six times against Rank 4: equivalent amounts of aggression between ranks.

It is useful at this point to describe and differentiate a third alternative dominance structure used in this study: curvilinear structure. For this study, a curvilinear dominance structure was created by using a logarithmic transformation on the rectilinear dominance ranks. A curvilinear dominance structure is an intermediate between despotism and rectilinear dominance in that it allows for larger distances between the top ranks and smaller more insignificant differences between the bottom ranks. A curvilinear dominance structure conveys less social complexity than a rectilinear structure, by approaching a more despotic formation by giving the top ranks more weight than the lower ranks. Although mathematically a more complex formulation (Cohen & Cohen, 1983), a curvilinear dominance structure is intermediate in social complexity, and for this study it will be characterized as such. These three dominance structures provide testable models for the expression of dominance in crickets, without constraining their behavior patterns into any specific pattern common in much of the dominance literature. These three discrete dominance structures are important in terms of testing the meaning of dominance status or rank. In much of the cricket literature actually dealing with dominance hierarchies of groups (many cricket studies use the dominant-subordinate

designation to signify residency of a territory), the linear dominance structures are implied to be interval orders when, in fact, they are only ordinal orders (Chankshaw, 1979; Phillip & Konishi, 1973).

In terms of dominance status, a male's competitive ability may depend on such variables as size, age, previous experience, pugnacity, ability to sing, and investment patterns (attachment to a site) (Alexander, 1961; Boake & Capranica, 1982; Cade, 1979; Darwin, 1871; Wilson, 1975). Research in the field of cricket dominance hierarchies is limited; as stated before, many studies confound territorial residency with dominance. In addition, many studies have determined dominance ranks based on fights between dyad pairs and not in interactive dominance groups (Adamo & Hoy, 1995; Latimer & Sippel, 1986). Dominance ranks based on dyad pairs is less direct and more inferential in determining a group dominance hierarchy. A possible limitation to these studies is the work on agonistic refractory periods in *G bimaculatus* by Adamo and Hoy (1995): crickets regain aggressive tendencies after 10 minutes. Alexander (1961) found in *G. veletis*, that age but not size influenced male aggressive behavior. Cade (1979) found no effects of age or size in *G. integer*. Boake and Capranica (1982) found in the gregarious cricket, *Amphiacusta maya*, that calling song by dominants suppresses aggressive attacks by subordinates. Crankshaw

(1979) determined that the female house crickets were 60% more likely to mate with higher ranking males.

An intermale interaction event was introduced into the present study to test the effects of intermale competition for dominance status with a two-fold purpose: (1) the competitive interactions between the males may result in changes of song characteristics relevant to female choice (i.e. males may communicate status as reported by Crankshaw, 1979), and (2) competitive interactions may result in changes in singing behavior (as reported by Cade, 1979, males may adopt alternative strategies). These purposes generate several hypotheses to be evaluated concerning dominance structure in crickets and its relevance to calling song characteristics and singing activity.

Specific Hypotheses Related to Male Competition

Of primary concern to this study was the possibility of modifications to the calling song characteristics following a intermale competitive experience. This prospect required a definitive look into the relationship between male competition and changes in male calling song components. In order to determine if dominance status was a phenotypic variable that could be signaled to females, it first had to be determined that it exists in crickets. Second, the structure of the dominance relationships had to be characterized to determine the meaningfulness of rank.

Finally, the role of dominance in the dynamics of calling and competition had to be determined. Dominance may have multiple effects on singing behavior and calling song components. These are important questions to ask because they affect the communicative nature of the calling song. First, events during the intermale interactions had to be measured. What was the outcome of the intermale competition? A few possible outcomes were suggested in the literature: (1) despotism (Wilson, 1975), (2) linear dominance hierarchies (Alexander, 1961; Crankshaw, 1979), (3) alternative calling and noncalling strategies (Cade, 1979). The nature and outcome of intermale competition warranted an in-depth evaluation.

(1) The first set of hypotheses related to dominance structure in the house cricket. Based on the gregarious "lekking" nature of *A. domesticus*, dominance relationships are most likely the primary outcome of intermale competition (Crankshaw, 1979). Based on these considerations, three forms of dominance structures were considered: despotism, curvilinear hierarchies, and rectilinear hierarchies. The structure of the dominance relationships determines the characterization of the ranks within the dominance structure. Rank characterization is necessary for determining the effects of the level of rank on the crickets and their song characteristics. If the structure of the cricket groups represents a despotic hierarchy, then the ranks of 2, 3, and

4 contribute no information as to what is being signaled in the song components. If ranks are meaningful, then specifying how each rank affects the crickets is necessary. Based on these results, the individual ranks of the crickets in their competitive groups were assigned. The effect of group was statistically controlled.

(2) The second set of hypotheses concerned the effects of dominance on singing behavior. The control of singing behavior is the control of "access" to females. There are several hypotheses to be considered concerning the effect of dominance status on singing activity. As discussed by Cade (1979) and reviewed above, there are several possible alternatives to calling behavior. In *A. domesticus*, the hypothesized control mechanism to affect singing behavior and activity in rival males is the dominance relationships among them. The null hypothesis is that dominance relationships have no affect on singing activity. However, several studies in the field have disproved this hypothesis, and demonstrated that dominance interactions affect singing behavior and activity. For this study, the dominance interactions were hypothesized to have the specific effect of suppressing singing activity in subordinates, resulting in subordinates adopting alternative singing and nonsinging strategies (as identified by Cade, 1979) based on descending dominance rank. To summarize, subordinates were expected to adopt one or more of the following alternative strategies: reduced song

intensities, altered singing times, or cessation of singing altogether. In addition, it was suspected that the competitive interactions would be harsher on subordinates, resulting in higher attrition rates among lower ranking individuals.

(3) The third set of hypotheses related to changes in the calling song characteristics from before and after the intermale competitive interactions. Males may signal their dominance rank. The song characteristics were evaluated for changes between the isolated-male and post-competitive conditions, and for correspondence to the dominance structure and ranks of the individuals. In addition, it was hypothesized that dominance was signaled in addition to the phenotypic female choice parameters.

Research Traditions Within the field of Cricket Bioacoustics

The ability of crickets to produce and perceive acoustic signals has led to a substantial amount work in the field of behavioral biology to determine how these tiny nervous systems deal with this seemingly sophisticated ability. As Scott (1958) noted, highly developed sound-perceiving organs were for the most part only found among vertebrates, with crickets and grasshoppers being an invertebrate exception. The issue of how crickets have managed sound production and perception became a primary concern to early behavioral

biologists. Due to the ease of housing, handling, and rearing crickets, they became a principal resource for the study of sound perception in animals. Moreover, the nervous systems of these invertebrate species were perceived to be simple and the determination of how sound is perceived by crickets easily ascertainable. Two research traditions out of the field of behavioral biology predominated in the study of cricket bioacoustics: ethology and sociobiology. These two differing perspectives affected how and what each tradition investigated in the issues involved in acoustic communication.

The ethological research tradition predominated in the earliest studies of cricket song, taking a primarily neurophysiological approach. Ethology is based on the "naturalistic study of whole patterns of animal behavior," and classical ethology was based for the most part on a group selectionist paradigm (Wilson, 1975, pp. 6). The primary focus of classical ethology was on the mutually beneficial use of song for sexual attraction and reproduction. Natural selection in this sense would cause crickets to evolve an optimal species-specific song for use by the females. The perceived functioning of acoustic signaling in crickets was bringing together males and females for reproductive purposes. On the other hand, sociobiology, based primarily on an individual selectionist paradigm, saw cricket calling song as a potential means for individual phenotypes (the

product of their genes) to monopolize the mechanisms of sexual selection for individual advantage. The assumptions of classical ethology led to a focus on species-specificity, and the assumptions of sociobiology led to a focus on individual differences and potentiation.

Classical ethology was primarily concerned with species-specific whole animal behavior and the mutually beneficial communicative purposes of calling song. Classical ethologists perceived calling song as a primary way to insure species-specific interactions between males and females. It was not surprising then that they focused on the perception capabilities of the females to the species-specific characteristics of male calling song. As Ewing (1989) acknowledges, when the interest is in the neuronal circuits and elements involved in song recognition, it is practical to concentrate on the essential features of the song. The ethology research tradition pursued the processes and mechanisms of species recognition, while the sociobiological research tradition pursued mate choice.

Sociobiology (Wilson, 1975), born out of evolutionary biology, took up the individual selectionist basis for the utilization and selective maintenance of the communicative capacities of cricket song. Within sociobiology was the notion of evolutionary change through individual differences and sexual selection. Male calling song in crickets was said to be used by females not only for species recognition, but

also for mate choice. Sociobiology focused on the differential reproductive benefits to female fickleness and male advertisement. Within the sociobiological research tradition, the intraspecific variation between songs of different males was a potential source of information about the physical suitability of the male, which was as important to females as species-specificity. (Forrest, 1983; Gwynne, 1982; Hedrick, 1986; Stout, et al., 1983). A third function for components of male calling song was linked to the two initial ones: the signaling of male's phenotypic traits that signify genetic fitness. Calling song provided a primary cue not only for mate location and identity by the female, but also potentially indicated features of male genetic quality (Bailey & Yeoh, 1988; Crankshaw, 1979; Gwynne, 1982; Hedrick, 1986; Simmons, 1988a). The ranges of song parameters that elicited female phonotaxis were sufficiently large to allow substantial inter-individual variation within the species-specific envelope. To this end, recent studies including this present study were attempts to match song features to the phenotypic traits of the males.

Concern in the classical ethology research tradition centered around determining the stimuli necessary and sufficient to elicit phonotaxis in females. It was assumed that all males had evolved to one species-typical pattern that maximized female attraction and phonotaxis. Within this tradition were techniques that focused on the simple

structures of species-specific characteristics of song. The classical ethology research tradition was unconcerned about trait differences other than species. Individual variations in song characteristics were considered to be random errors in song delivery. Within a species-specific paradigm, individual differences in song variability was disregarded, since it was held that song variabilities do not contribute to the understanding of species recognition. Focusing on song consistencies and species-typical components, neuroethologists looked to determine the underlying mechanisms for sound perception and recognition.

Neuroethologists (Bentley, 1977; Huber, 1962, 1978; Kutsch & Otto, 1972; Pollack & Hoy, 1979; Thorson, Weger, & Huber, 1982; Walker, 1962) set about to identify the underlying physiological mechanisms controlling the production and perception of cricket song. These early investigators were primarily interested in the neurobiology of the cricket's auditory perceptual system. Within this framework, the primary concern was the two 'essential' features of cricket song: (1) species identity and, (2) location (Cade, 1979; Huber, 1962; Walker, 1962). They proposed that acoustic communication signals would function as efficiently and economically as possible, with all males optimally adapted to sing all the relevant song characteristics. The critical features of calling song would be relatively invariant between males, since deviations would

result in species misidentification causing a decline in the population. These researchers hypothesized that a limited set of song components would communicate the critical features of species identity. Underlying their hypotheses, was the belief that a limited set of neurons would be found that responded directly to the critical features of the calling song. As stated by Doherty and Hoy (1985, pp. 458)

[These studies postulated that] "elements that are common to both sender and receiver mechanisms may be single neurons or networks of neurons involved both in the generation of temporally patterned signals (i. e., central pattern generators) and in the recognition of these temporal patterns (i.e., neural filters and sensory-motor templates)...that serves as a species-specific temporal pattern filter or sensory-template for recognizing a signal."

Based on this idea, investigators set out to determine the properties of calling song that were important for triggering this "neuronal recognition-template." It follows then that they looked for the eliciting stimulus necessary and sufficient for phonotaxis in females. Studies were designed to characterize the species-specific features of cricket song. The most extreme hypothesis out of this body of work was the *30-Hz hypothesis*: the syllable repetition rate was deemed necessary and sufficient to elicit neuronal recognition of male song (in *Gryllus campestris* L.) (Huber,

1962; Thorson, et al., 1982; Walker, 1962). However, this hypothesis soon came under attack because it became evident that no 30-hz template was to be found and, additionally, the 30-Hz syllable repetition rate was not all sufficient to elicit phonotaxis (Doherty & Hoy, 1985). It became evident that species differences were dramatic as far as song recognition specifications were concerned. The syllable repetition rate may have been highly important to *G. campestris*, (albeit not sufficient), but this finding was not as universal as supposed. Even within the neuroethology field, it became evident that sound perception in cricket was not so simple. A new theory was proposed that extended the 30-Hz hypothesis notion: the "trade-off" hypothesis (Doherty & Hoy, 1985).

"the 'trade-off' hypothesis states that several temporal properties of the calling song contribute to the total attractiveness of the acoustic stimulus... each temporal property is a function of its presumed 'weighting' in the recognition process and of how well its value matches its presumed, optimal (tuned) value of the receiver" (Doherty & Hoy, 1985, pp. 464).

A later study by Stout et al. (1983) confirmed and extended this hypothesis by determining that *A. domesticus* females evaluated all the relevant properties of male calling song, including frequency and intensity properties. This extended the "trade-off" hypothesis by including frequency and

intensity song parameters into the recognition process. Stout et al. found that as the song parameters deviated from model calling song, females responsiveness decreased. Stout et al. listed the specific limits to the song parameters that female house crickets would allow. These song parameters were syllable period (preference $50 \text{ ms} \pm 10 \text{ ms}$), syllable duration (preference $25 \text{ ms} \pm 5 \text{ ms}$), number of syllables (preference 3 syl), chirp rate (preference 1.5-2/s), frequency (preference 4-5 kHz) and intensity (preference 45-85 dB).

It is germane to note that no "calling song recognition-template" neurons have been found in the cricket auditory neurobiology (Huber & Thorson, 1985). The auditory neurons and interneurons respond to varying fields of cricket calling song, many of which overlap. All auditory neurons and interneurons eventually synapse in the head ganglion, apparently for integration of the various response fields of the auditory neurons. This implies that a more critical evaluation of calling song is occurring within the females' neurobiology that goes beyond mere recognition, and that entirely reflexive phonotaxis does not occur. This finding supports the work of sociobiological researchers: some cricket calling song characteristics will be invariant. To facilitate recognition of species, however, within the species, individual variations in the song components will signal individual variations in male phenotypic quality.

Many current studies in the field of cricket bioacoustics are pursuing the issues of sexual selection in cricket calling behavior. Even a look at the findings of Stout et al. (1983) indicates that the "model" *A. domesticus* song characteristics have a sufficient range to allow for individual differences without falling out of the "species-specific range. This leaves substantial room for inter-individual variation. New studies are evaluating even finer structures of male calling song as the technology advances. These studies are attempting to establish correlations between the male morphology, behavior, and environment to calling song components (Cade, 1979; Ciceran et al., 1994; Simmons, 1988a, 1995; Walker, 1962). Many of these studies may be limited by looking at too few song components or male characteristics. A pronounced number of these will look at a single male physical trait (Simmons, 1988a).

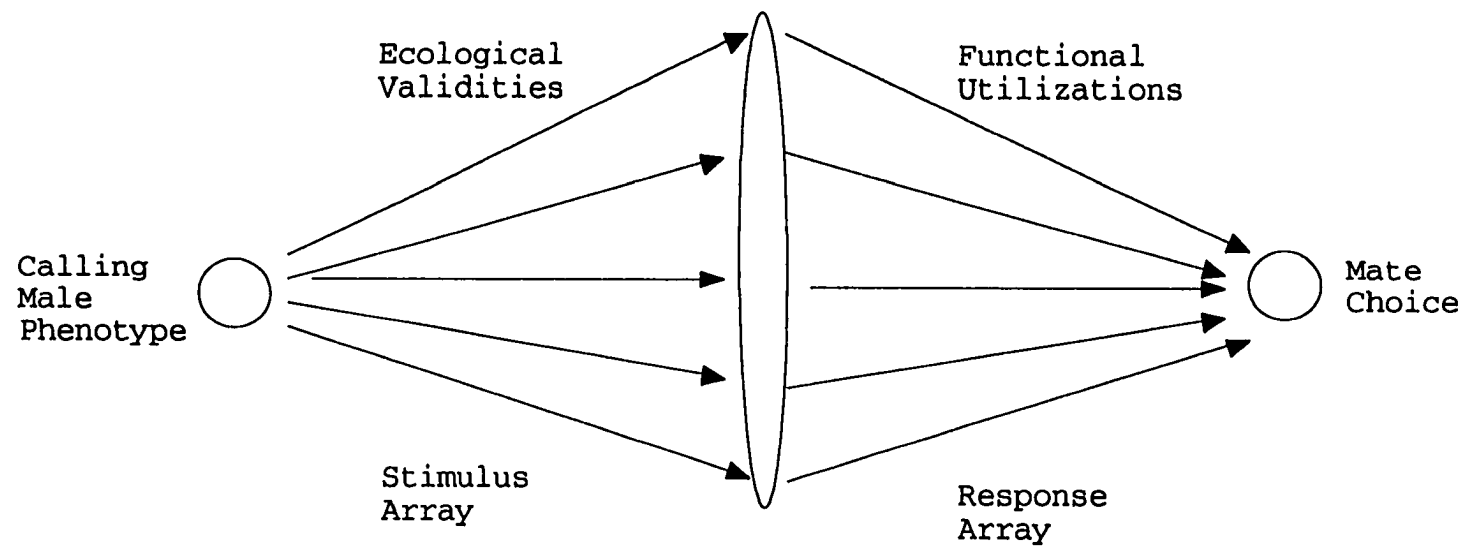
Rationale for Present Study

As presented in the Introduction, the modeling of female mate choice has proven challenging. Assessment of female choice has proven elusive to many researchers because female choice is made up of not only female mating responses, but also the male stimuli (male mate quality signaling) to which the female responds. Female choice involves complex relationships between the dimensions of intermale

competition, male phenotypic signaling, female-male interactions, and finally, female mating responses. The primary difficulty has been in modeling all of these various dimensions in a single representative framework.

This study proposes the use of a Probabilistic Functionalism/Brunswikian Lens Model (described by Petrinovich, 1979) as a conceptual framework to model the multivariate and dynamic array of male mate quality cues (and female choice responses) necessary in the specification of female mate choice. A Lens Model framework of female mate choice is illustrated in Figure 2. On the left side of the lens is the male cricket's mate quality which serves as the distal stimulus. Emanating from the distal stimulus is a stimulus array of song parameters that serve as the proximal cues to male mate quality. These cues interface with the female's sensory and central neurobiology (represented here by the lens). Refracting from the lens is an array of behavior responses the female can make based on the information conveyed via the song parameters. These responses converge on the female's final mating decision, the distal achievement. By using this framework, female choice is fully modeled by linking female responses to the stimuli she receives. Moreover, the stimuli can be hierarchically ordered based on their trustworthiness or ecological validity as cues to male mate quality. The female responses can be ordered based on how likely the female will use a particular

Figure 2: Probabilistic Functionalism: The Lens Model



response (functional utilizations) based on the song cues she receives.

The rationale for use of the Lens Model was to provide a representative framework for evaluating male signaling of mate quality within the female choice model. A representative design was achieved by: (1) identifying and measuring as many relevant (theoretically specified) variables as possible; (2) retaining and modeling the relationships between the male's phenotypic profile and his song characteristics; (3) interrelating the multiple phenotypic traits; (4) interrelating the multiple song characteristics; and (5) sampling phenotypic and song characteristics on multiple occasions. Note that this study's focus was on male mate quality signaling, for that reason female responses were not specified.

Crickets are a logical choice to model and test female choice theories. (1) The crickets' songs can be isolated from the actual physical features of the males. (2) The males and females are not in any visual, olfactory, or tactile contact when initial mating responses are made, such that all mate related information the females receives is contained in song. (3) Clearly for economics sake, the most pure cues for female choice should be contained in song since song is vitally important for female mating decisions and selective forces would optimize effectual information. Finally as a comparative model, (4) crickets serve as models

for how evolutionary mechanisms work and can be readily applied to more complex systems (Huber & Thorson, 1985). The basic principles of evolutionary influences on behavior that can be applied to these insect systems will contribute to the knowledge base of how small nervous systems cope with big problems and will eventually shed light on the basic evolutionary principles influencing the nervous system. Since evolutionary mechanisms are universal, the basic rules that govern the nervous system are to be found in the simple insect systems.

House crickets (*A. domesticus*) have a particular usefulness for testing of male sexual signaling, female choice, and intermale competition. (1) House crickets are inexpensive, and easily acquired from local pet stores and reared in the laboratory. (2) Cricket calling songs are active at a distance, such that male acoustic signaling is separated from their actual physical presence. In addition, the high energy expense for acoustic signaling selects for honest signaling of male quality and female preferences for the song components that indicate quality. (3) Calling songs can be recorded, analyzed, and stored relatively easily and economically. Recording devices and sound analysis software are readily available. (4) *A. domesticus* males do not provide substantial spermatophores or nuptial gifts that may confound female choice for high genetic quality in males (Stout et al., 1983). The need for collecting and assessing

spermatophores as part of male phenotypic quality is eliminated. (5) *A. domesticus* are more gregarious and can be readily placed in a crowded chamber to facilitate intermale competition without causing unduly high attrition rates.

The crickets for this study were obtained from a local pet store, which obtained their crickets from local cricket farms. These farms rear crickets in captivity and in more crowded conditions than would be found in the crickets' natural setting. These conditions lead to stronger sexual selection and more inbreeding than natural populations. Such rearing conditions lead to smaller genetic and phenotypic variation among the males in the population. The males in this study were bred in such conditions, which would result in smaller intermale variance and underestimated coefficients of relatedness between the phenotypic traits and the song characteristics.

Several avenues into this complex system of male signaling of mate quality were taken. First, the male crickets were followed longitudinally. One hundred unmated male crickets were evaluated from final molt, to onset of singing, to multiple singing bouts under different environmental influences (e.g., before and after intermale competition), and some to death. Second, each individual male's calling song was repeatedly recorded on four occasions. Third, all males encountered both isolated and crowded (competitive) environmental conditions. Longitudinal

presentation of males into these two environmental conditions, allowed the researcher to possibly differentiate male signaling of female choice parameters in calling song from competitive changes to song. Finally, this study evaluated the multiple physiological characteristics of the male cricket as specified by sexual selection theory: which included physical measures of size, weight, length, color type, body intactness, and fluctuating asymmetry; behavioral measures of proclivity to sing, and time of singing; social measures of dominance relationships; and the life history measure of age at all times in the study.

Plan Of Research

The primary objective for undertaking this research was to uncover what information male house crickets, *Acheta domesticus*, were signaling in their calling song. Acoustic signaling involves both the information being communicated and the sound media through which that information is conveyed (Ewing, 1989). To uncover what information males are signaling via their calling song, a correspondence between the song characteristics and the information conveyed must be determined. However, what specific information is important enough to crickets that it would be signaled via calling song? To answer this question, a theoretical basis for the role of acoustic signaling must be decided upon.

Cricket calling song has been unequivocally linked to sexual attraction of females and to competition with rival males; two premises embodied by the theory of sexual selection (Darwin, 1871; Ewing, 1989). Thus, theoretical predictions as to the information that might be contained in cricket song can be derived from sexual selection theory.

Certain environmental conditions had to be contrived to distinguish between the two facets of sexual selection. First, calling song production had to be divorced from a competitive environment to one that would promote circumstances more conducive to female choice. Second, possible changes to male calling song had to be noted following a male competitive environment and differentiated from the female choice parameters uncovered in the noncompetitive environment. These were the two primary goals of this research design: (1) isolate individual males from competitive interactions and determine what their calling songs might be communicating; (2) create competitive encounters between the males and determine whether or not there were changes to their calling songs following these encounters and what the changed calling songs then conveyed.

Predictions as to the information being signaled in male calling song were derived from sexual selection theory. Isolated males encounter no interference from other males and do not either know or need to enforce their competitive status. Conditions of social isolation provide an optimal

situation for males to maximize the broadcasting of information most relevant to females. Isolated males can advertise "pure" female choice relevant information (song characteristics uncontaminated by competitive functions). Following intermale competition, males may presumably both have and realize their competitive status. The type of information to be conveyed via song has changed, since rival males must now be kept at bay, and females may seek information about each male's competitive relationships with the other males.

The first goal of this study was to identify potential female choice parameters advertised in male calling song. Sexual selection theory was used to provide several predictions as to what information would be most important to females that may be conveyed via isolated male calling song. Physical, morphological, and behavioral traits that are probable female choice parameters were specified as male size, body intactness, body asymmetry, color morphology, age, synchrony with female peak receptivity times, and male singing latency. Psychometric analyses were then performed on these morphological, physical, and behavioral traits in order to construct and test composite indices for these traits.

Male crickets were isolated from other males and their song characteristics were recorded. These song characteristics were subjected to sonographic analyses and

characterized by their component parts. These component parts were quantified and served as numerical indices for the sonographic isolated-male calling song characteristics. Using generalizability analysis, several aspects of isolated-male calling song were determined to be important individual male song characteristics and separated from those invariant song characteristics attributable to species-typical patterns. Isolated-male calling song factors (latent variables) were constructed by exploratory factor analysis using these indices. The isolated-male calling song factors were then predicted by hierarchical general linear modeling using the physical, morphological, and behavior traits specified by sexual selection theory.

The second goal of this study was to determine the effects of intermale competition on calling song and singing activity. Predictions as to the type of information being signaled in post-competitive male calling song were derived from sexual selection theory. Several things have changed for the males after intermale competition. Of particular interest are the social effects. After competitive interactions, males have agonistic and possibly status relationships with other rival males. These relationships require characterization in order to determine how they affect subsequent singing activity and calling song characteristics.

Sexual selection theory was used to provide several predictions as to what social behavioral traits may be relevant to intermale competition and may be important information to be conveyed to females via post-competitive male calling song. Since, house crickets, *A. domesticus*, are more gregarious and tend to live in groups, sexual selection theory suggested that dominance relationships may arise through agonistic encounters involving aggressive and submissive behaviors, and be influential in affecting male calling song characteristics. These dominance-related behaviors were recorded systematically by quantitative ethograms and by subjective ratings of competitive dominance rank. Psychometric analyses were performed on these social behavioral traits in order to meet three objectives: (1) construct and test common factors for the observed aggressive and submissive behaviors; (2) validate the subjective rankings of dominance with the observed behavior factors; and (3) explore alternative function forms of subjective dominance rank to reflect different hypotheses regarding cricket social structure. Generalizability analyses were performed to determine interobserver reliabilities, inter-item consistencies and temporal stabilities of both the observed behavior factors and the subjectively rated dominance ranks.

Following the intermale competitive interactions, male calling song characteristics were recorded again. Post-

competitive calling song characteristics were subjected to sonographic analyses and characterized by their component parts. Post-competitive male calling song factors (latent variables) were constructed by exploratory factor analysis using these aggregated indices. All the psychometric analyses performed for isolated-male calling song were repeated for post-competitive male calling song. The post-competitive male calling song factors were then predicted by hierarchical general linear modeling using the post-competitive social behavioral, physical, and morphological traits specified by sexual selection theory.

Hypotheses Addressed by this Study

The omnibus null hypothesis for this study is that the song characteristics of cricket calling song convey no information about the male crickets. This null condition literally says that cricket song is merely sound generated without communicative purpose, but it has been empirically disconfirmed by all studies in the field which verify species-typical characteristics in calling song, and phonotactic responses by conspecific females to these song characteristics. The classical ethology alternative hypothesis is that calling song characteristics convey information of simplest content, that of species only. Since the species-specific nature of calling song has already been

established, this will serve as the de facto null hypothesis for this study. This study proposes an alternative hypothesis derived from sexual selection theory: that male calling song characteristics convey information about the individual male's attributes, specifically those attributes conveying information about male genotypic fitness. As specified by sexual selection theory and, more specifically, female choice theory, calling song characteristics should convey information about the male's (1) size, (2) body symmetry, (3) body quality, (4) age, (5) sexual motivation, and (6) social dominance status. All of these phenotypic features have been theoretically specified as being indicators of fitness-related genetic quality in males. To summarize briefly, male size has been linked to the lack of developmental difficulties, pathogen and parasite resistance, superior foraging abilities, greater strength and competitive abilities, and larger sperm loads. Body symmetry has been linked to strong immune function and lack of developmental stress (Parsons, 1990; Thornhill, 1993). Body quality also indicates the lack of developmental difficulties and the ability to avoid physical injury or sustain bodily damage due to environmental and competitive events (Thornhill & Alcock, 1989). Age is indicative of health and survival ability (Alexander, 1961; Halliday, 1983). Sexual motivation is indicative of androgen levels which contribute to competitive abilities and sperm load (Wilson, 1975). Lastly, social

dominance status is indicative to the multifaceted competitive abilities and trait necessary to best rivals. Dominance status may further be linked to size, body symmetry and quality, and sexual motivation. Within the domain of social dominance, several secondary hypotheses regarding dominance structure and behavioral alterations in singing activity were presented earlier and will be examined in this study.

Organization Of Dissertation

Because several similar procedures were applied to both the first and second goals of this study, the present dissertation is organized by these procedures rather than the ultimate objectives. The separate results for the first and second objectives are presented in parallel within each of these procedural divisions. The first stated objective--the signaling of female choice parameters--was the principal topic of a previously submitted Masters thesis (Sage, 1996).

In order to follow the logic of the steps taken to obtain the physical factors, behavior factors, and song characteristics factors, much of the Masters thesis is restated for this doctoral dissertation, in particular, the logical order of the experimental procedures and the analyses and rationale for generating song factors. Because an understanding of these results is necessary for the complete

comprehension of the subsequent doctoral work, certain sections of the Masters thesis were reproduced in the present dissertation and will be specifically identified below. Some of these sections were essentially unmodified, but others were either partially or completely revised in light of the new findings. Because the results of the Masters thesis indicated the great importance of intermale competition in affecting cricket calling song, these findings set the stage for the work continued in the present dissertation. The dissertation proper was primarily concerned with the second stated objective, the influence of intermale competition on song, and entirely new sections have been written to address these issues.

Throughout the following description of the dissertation, the level of revision that each section underwent will be indicated as follows: (1) written originally for the present dissertation, (2) reproduced with major revisions, (3) reproduced with minor revisions, (4) reproduced essentially without modification. These labels will clearly identify the provenance of each section and help distinguish between the work completed for the Masters and that further work completed for the dissertation without unduly obstructing the flow of the manuscript. This section is provided to specifically denote the provenance of each

section of this dissertation and highlight sections original to the dissertation.

The Introduction section as a whole has been reorganized and several new sections have been added: (1) a plan of research, (2) an introduction to cricket song, (3) a summary of intermale competition including sections dealing with dominance structure and agonistic behavior in crickets, and (4) summation of the major hypotheses tested by this study. Several sections from the Masters thesis were utilized with major content revisions and reorganizations: (1) a summary of sexual selection, (2) a summary of female choice selection and its relation to male calling song, (3) a review of the research traditions in cricket bioacoustics, and (4) a discussion of the purpose of this study.

The Methods section has been reorganized and several new subsections have been added: (1) in the Apparatus subsection, a description of the video-recording and observation equipment, (2) in the Procedures subsection, a description of the human observer training and the social behavioral measures taken, (3) in the Statistical Analyses subsection, a description of the psychometric analyses of the observed behaviors and dominance rank measures, and the structural modeling of post-competitive male calling song. Sections in the Methods that involved major revisions were (1) the description of the morphological measurements, (2) the organization of the Procedures subsections, (3) the

sonographic analyses of the calling songs. Sections in the Methods that involved minor revisions were (1) the description of the subjects, (2) a description of the audio-recordings in the procedures, and (3) the generalizability analysis and the exploratory factor analyses of the song characteristics. One section in the Methods that was relatively unmodified from the Masters thesis was the structural modeling of the isolated male calling songs.

The Results section has been reorganized and three new subsections have been added: (1) the psychometric analyses of the intermale competitive behavioral and dominance phenotypic aspects, (2) the psychometric analyses of the morphological phenotypic aspects, and (3) the prediction of post-competitive male calling song characteristics with other phenotypic traits. Subsections in the Results that had minor revisions from the Masters thesis were (1) the between-chirp and within-chirp song consistencies, (2) the determination of the song factors, and (3) the prediction of isolated male calling song characteristics with other phenotypic traits.

The Discussion section has been reorganized and underwent major revision. Subsections were added to denote major topics: (1) social dominance in house crickets, (2) individual differences in phenotypic attributes and song characteristics, (3) signaling of female choice parameters in isolated-male calling song, and (4) signaling of social dominance and male phenotypic attributes in post-competitive

calling song. Subsections in the Discussion that underwent major modifications from the Masters thesis, to include new post-competitive results: (1) Individual differences in phenotypic attributes and song characteristics, and (2) signaled female choice parameters in isolated-male calling song. A new Future Directions section was added.

METHODS

Subjects

Male crickets (*Acheta domesticus*) were purchased from a local pet store as nymphs in their final instar. Crickets were maintained at 76° F with an approximately 65% relative humidity on a 12/12 hour light:dark cycle. Crickets were fed cricket chow, crushed dogfood (Nutra Nuggets®), apples, and water ad libitum. Red lighting was used in all laboratory rooms during the crickets' dark cycle, allowing personnel to work without disturbing the crickets.

Nymphs were housed as a colony in several large plastic aquariums (40 cm x 20 cm x 40 cm). Each aquarium contained a 1" layer of sand, a watering sponge (5 cm x 5 cm) in a petri dish, a petri dish (10 cm) containing food, and three to five peat pots that served as shelter for the colony. Nymph numbers in the colony chambers did not exceed fifty individuals per chamber. This procedure avoided crowded conditions that often result in differential developmental adaptations. Crickets were checked daily for their final molt into adults. Newly-emerged adult males were removed and placed in individual housing units (plastic shoeboxes) equipped with 1 cm layer of sand, a watering sponge (2.5 cm x 2.5 cm) and food held in small petri dishes, and one paper egg carton cup for shelter. Each individual unit was labeled

with the cricket's identification number and date of final molt.

Solitary crickets were kept in their individual containers, but were housed in a single colony room. Crickets were isolated from tactile contact from conspecifics but could potentially see, hear, or smell other crickets in the colony room. Tactile contact between crickets was limited to the 48 hour competitive interaction period of the study. All males remained unmated throughout the study.

Intermale competitive interactions occurred in a round (18 cm diameter by 10 cm depth) plastic container covered with a transparent piece of plastic glazing. This competitive arena contained a 1 cm layer of sand, a small watering sponge (2.5 cm X 2.5 cm) in a petri dish, and one kernel of dogfood. Small matchboxes were placed in the arena for shelter, between video-recordings.

In spite of the enriched environment provided, subject attrition rates were high. Approximately fifty percent of all the crickets purchased failed to be used the study, usually dying before being audio-recorded. This high attrition rate also affected the experimental subjects, such that several did not complete all levels of the study. Although the target number of subjects for this study was 100, only 62 completed all aspects of the three experimental conditions: (1) audio-recorded isolated male calling song, (2) social interactions in the competitive arena, and (3)

audio-recorded post-competitive calling song. Seventy four crickets completed at least one song in both audio-recorded experimental conditions and socially interacted in the competitive arena. Ninety nine crickets sang at least two songs, such that they had repeated measures. The ages of the experimental males ranged from 4 - 123 days old throughout the experiment.

Apparatus

All audio recordings were made using a Sony TCD-D3 DAT Walkman Recorder, with a DAK UEM83R Superdirectional Shotgun microphone. A sound reducing chamber was used to limit the background noise in the audio recordings. The sound chamber consisted of a cardboard box (60 cm X 35 cm X 35 cm) lined with 10 cm acoustic foam. A 5 cm hole in the top of the box allowed the microphone to be placed in the center of the chamber. A cardboard door, lined with the 4" acoustic foam, on the side of the sound chamber (25 cm X 25 cm) allowed one housing unit to slide into the box. One housing unit lid was made permeable to sound by cutting the top off the lid and gluing in fiberglass screening. This lid was used on the individual housing units during audio recordings.

Video recordings of the social competitive interactions were done in a dimly lit recording room using a Panasonic VHS video camera. Recorded on the bottom of the videotaped

session was the time in hundredths of a second, using a Sony video- timer. Videotapes were labeled with an identification letter (A through Z) for the group, and the identification number and the label designation of each cricket within the group. The primary observer used an Emerson model TC1960 television monitor with a Zenith VR4226HF VHS video-cassette recorder, capable of frame-to-frame viewing, to view the videotapes. Other observers used their own personal television monitors and video-cassette recorders, all equipped with slow motion capabilities, to view the videotapes. A scale accurate to 0.001 mg was used to make body weight measurements. A Bausch & Lomb Model ASZ30L3 dissecting microscope was used to observe and measure length and physical characteristics. All the cricket physical and recorded song data were recorded into a logbook.

Procedures

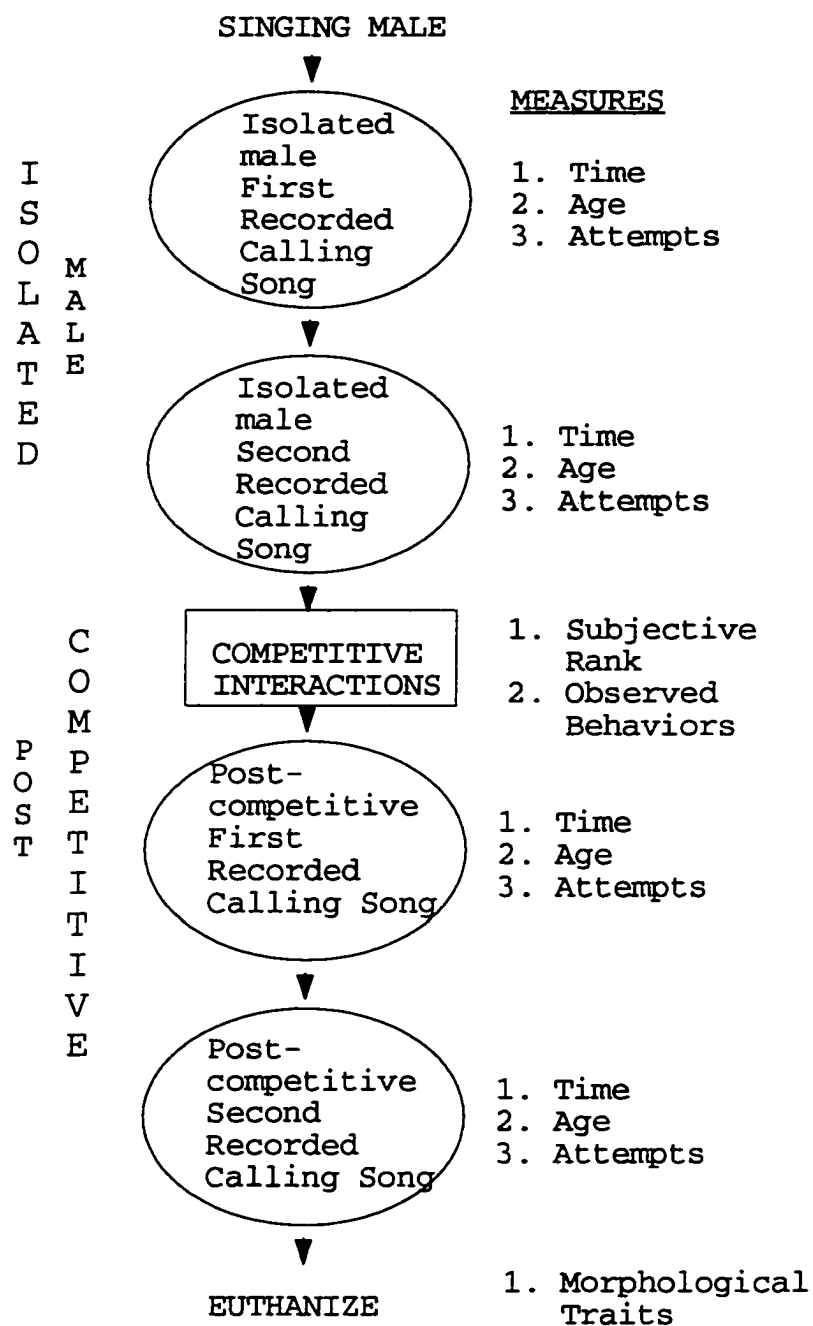
Design Overview

The colony room was divided into seven sections: one for the nymph colonies and six for each of the experimental sections (see Figure 1). Sections one through three housed males in the isolated male condition: (1) unrecorded, (2) recorded once in isolation, (3) recorded twice in isolation and ready for social competitive arena. Section four (4) housed males during the social competitive interactions.

Sections five and six housed males in the post-competitive condition: (5) recorded once post-competitive, (6) recorded twice post-competitive and ready for euthanization.

Newly emerged adult males were placed in Section 1 as 'unrecorded'. These unrecorded males were monitored daily at 0, 3 and 5 hours into the L:D cycle for singing in the colony room. Males found to be singing were identified by marking the lid of their housing unit with a music note symbol. These males were subsequently placed in the sound chamber, and an audio-recording was attempted. The experimental design involved recording the songs of 100 crickets on four occasions: twice while isolated and twice after being removed from the social competitive arena. A minimum of twenty-four hours was allowed to elapse between audio-recordings.

Isolated males with two recorded songs (completed sections 1-2) were placed in Section 3: 'ready for social competitive arena'. When four crickets were in Section 3, they were prepared for the social competitive arena. All four males were placed in small plastic vials (4 cm in diameter and 12 cm deep, and plugged by a sponge stopper) and chilled for three minutes. The chilled crickets were sluggish and easy to handle, yet unharmed. The crickets were labeled by supergluing tiny white paper tags with black contrasting markings (□, ▤, ■, or no label) on their thoraxes, these males were referred to as white, diagonal,

Figure 3: Methods Flow-chart

square, and blank, respectively. After warming up and resting for five minutes, the four crickets were placed into the competitive arena. The competitive arena was placed under the video camera and videotaped for one hour the video-recording room. The competitive arena was then removed from the video-recording room and returned to the colony room. Two match boxes were added to the arena to reduce bodily injury by lessening aggression between the crickets, and providing protection for the weaker or subordinate individuals. After 24 hours, the competitive interactions were again videotaped, this time for two hours. Immediately following the final videotaping, the males were removed from the competitive arena and returned to their individual containers. There were a total of 25 social competitive groups. After 24 hours, audio-recordings were resumed until two post-competitive songs were recorded or the cricket died.

Males completing the study were euthanized by overdosing with an anesthetic Fly Nap® (triethylamine). Euthanized crickets were subsequently weighed (wet weight), and their body lengths (wet length) measured. Cuticular color and physical condition were assessed under the dissecting microscope. Cricket bodies were put in sterile petri dishes and placed in a low-humidity (<10%) chamber. Cricket bodies were allowed to desiccate for thirty days. Crickets that died during the study were handled similarly. After thirty days, the cricket bodies were again weighed (dry weight) and

their body length (dry length) measured. The cricket bodies were retained for inter-cricket color comparisons by three independent raters, assessed after all males in the experiment had completed testing and had been desiccated.

A logbook recorded the date of final molt for each cricket; the date, time, and number of attempts for each audio-recording; the date and time of the social competitive videotapes; the date of euthanization; and any other information pertinent to the study such as losing a leg during labeling or dying during the study. The physical information obtained after euthanization was recorded in the logbook.

The primary criterion that placed a male into this study was having two songs recorded while isolated, the isolated-male condition. Four crickets, were exceptions to this criterion, were included in the study to represent possible 'non-singing' alternative strategies. Two unrecorded males were placed in competitive groups. Of these males, one never sang, the other one completed both post-competitive sections. Two males recorded only once were placed in the competitive groups because of the number of 'attempts' to record them a second time had failed. Both males completed both post-competitive sections. Competitive interactions were particularly harsh on the viability of the experimental crickets. Twenty-three crickets stopped singing after the

competitive interactions, and ten died during or soon afterwards.

Audio recordings

Although the sound chamber provided good audio recording conditions, the quietness inhibited the crickets from singing. Some form of soft background noise appeared to encourage the crickets to start singing. Crickets that did not readily sing within ten minutes time were softly hummed to, or read out loud to by the person recording. Once the crickets began singing, the recorder would stop humming or reading and begin the recording process.

Singing crickets were allowed to sing for 30 seconds before the audio recordings were begun. Crickets were audio-recorded for a two minute duration. If the cricket sang in brief bouts, the recorder would *PAUSE* the DAT during the time the cricket was not singing and wait for the cricket to resume singing. All recorded songs consisted of a minimum of 25 chirps. The time into the L:D cycle was recorded in the logbook for each recorded song. If, after twenty minutes a male had not sung, it was returned to the colony room. More attempts to record that cricket singing were made later that day. Cricket recordings continued to be attempted for up to seven hours. Males were checked at 0, 3, and 5 hours during the crickets' dark cycle. It is estimated that most of the songs were recorded within the first five hours. Recorded

isolated crickets were placed in Section 2 (recorded once) and given 24 hours before another recording was attempted. Singing crickets were audio recorded in this manner twice while isolated and twice post-competitively. The total number of attempts required to get a recording of a cricket's song was entered in the logbook.

Human Observer Training

Competitive interactions were observed by four trained observers who independently scored the behavioral activities of the crickets from the videotapes. One primary observer trained the three secondary observers and scored all twenty-five group videotapes. The three secondary observers scored eleven of the groups. The three secondary observers were trained by the primary in three one-hour sessions and were taught to identify cricket behaviors by observing multiple occurrences of each behavior on a practice videotape and by learning the behaviors' definitions from an ethogram. Following the initial training period, each observer was tested for reliability by scoring the behavioral interactions between the crickets in a five minute block of videotape that had been scored previously by the primary rater. Secondary observer scores were compared with the primary's scores. Observers were re-trained in 30 minute sessions for behaviors they scored poorly on. Observer training continued until scores of 95% correspondence with the primary's were

obtained. Training was usually completed within six practice blocks.

Measurement

The phenotypic attributes of the male crickets broke down into three categories: (1) the social dominance category involved features of the agonistic behavioral interactions between the males, (2) the physical traits category involved features affecting male singing behavior, and (3) the song characteristics category involved the acoustic features of the males' calling songs. The behavioral measures of the crickets' phenotypes were divided by the following three categories. (1) Those behavioral attributes associated with the males' agonistic interactions were placed within the social dominance category. (2) Those behavioral attributes associated with the males' singing activities were placed within the physical traits category. (3) The song characteristics category was made up of all the acoustical characteristics of the calling songs.

Social dominance measures of agonistic behavior. In order to measure how the crickets behaviorally interacted with conspecifics an ethogram, or systematic behavioral inventory was constructed by observing a large colony of crickets and identifying individual behavioral components. According to Figueredo, Petrinovich, & Ross (1992, pp. 413),

"An ethogram is a detailed list of all the fundamental behavioral elements that a species exhibits in a given situation, along with clear descriptive guidelines for assignment to and unequivocal discrimination between, elements." Previous studies such as Alexander's (1961) study of cricket behavior were consulted for terminology and cricket behavioral repertoire. An entire inventory of behaviors was obtained and is listed in Appendix B. From that ethogram, sixteen notably agonistically-related behaviors were selected and are listed on Table 1. These behaviors were selected because they involve (1) interindividual interactions and (2) aggressive and submissive responses. These behaviors were *a priori* placed into two behavioral factors (Table 1): 1) Aggression Factor and 2) Submission Factor. One notable exception from this list is fights. Although clearly aggressive in nature, it is nondirectional; the winner and loser is not determined until a terminating behavior occurs, usually a submissive response "withdrawals, from" (Alexander, 1961).

In order to quantify behavioral occurrences, a quantitative ethogram was acquired by "enumerating occurrences of each element [within the ethogram]" using 0-1 focal animal sampling (Figueredo et al., 1992).

Table 1

Cricket Ethogram for Aggression and Submission Factors

Behavior	Behavioral Definition
<u>Aggression Factor</u>	
Approaches	FA approaches NFA within one bodylength.
Charges	FA charges NFA in threat display.
Chases	FA chases NFA a distance greater than one bodylength.
Kicks	FA kicks NFA with leg(s).
Sing, rivalry	FA sings rivalry song at NF male.
Stands on	FA stands on NFA.
Supplants	FA forces off and overtakes area occupied by NFA.
Threatens	FA raises body and wings in threat display to NFA.
<u>Submission Factor</u>	
Is Approached	NFA approaches FA within one bodylength.
is charged	NFA charges FA in threat display.
is chased	NFA chases FA a distance greater than one bodylength.
is kicked	NFA kicks FA with leg(s).
is sung rivalry	NFA sings rivalry song at F male.
is stood on	NFA stands on FA.
is supplanted	NFA forces off and overtakes area occupied by FA.
is threatened	NFA raises body and wings in threat display to FA.

Note. FA = focal animal; NFA = nonfocal animal

Zero-one focus animal sampling is a technique for time sampling the occurrence and prevalence of observed behaviors of a focal animal. Zero-one sampling is accomplished by dividing an observation period into smaller time sampling intervals. The occurrence of a described behavior is determined as to whether (1) it occurred or not (0) in the preceding interval (Figueredo et al., 1992; Kraemer, 1979). At the end of the observation period, the 0-1 samples are summed across the intervals within the observation period. For this study, the observation period was six pre-selected 5 minute blocks within the videotapes, and the time sampling interval was specified as 30 seconds. For issues concerning the validity and reliability of these methods for obtaining a quantitative ethogram, consult Figueredo, Petrinovich, and Ross (1992).

The timed videotapes were divided into two sections, based on the two experimental time periods that were video-recorded: (1) the one hour dominance "formation" period, recorded when the crickets were initially placed in the competitive arena and (2) the two hour "stable" dominance period recorded after the crickets had been together for twenty-four hours. Three five-minute blocks were selected from each of the two sections on the timed videotape for a total for six observation periods. Minutes 0-5, 20-25, and 50-55 (designated blocks one, two, and three respectively) were selected from the one hour "dominance formation" period.

Minutes 10-15, 50-55, and 1:30-1:35 (designated blocks four, five, and six) were selected from the two hour "stable dominance" period. Observed behavior scores were obtained by using the described 0-1 focus animal sampling at 30 second intervals for each block for each of the sixteen behaviors (see Table 1). Observers timed the sampling intervals using the time recorded on the videotapes. Having the time taped on the videotape allowed for replication of the focal cricket's scores by insuring that independent observers scored the exact same time intervals. Observers scored each behavior by marking down its 0-1 sampled occurrence on the focal cricket's datasheet.

The dominance status of each male cricket was assessed both by examining their observed behavior scores and by subjective ranking of the human observers. Subjective ranks were obtained by observing the videotape of a group of crickets and then subjectively, without any alternative measurement of behavior, deciding the rank of each individual. Subjective human rankings of dominance status provide highly similar dominance structural outcomes as large statistical ranking matrices for primates (Bramblett, 1981). In terms of cricket behavior, Alexander (1961, pp. 142-143) states "dominance order is usually obvious within a few minutes after beginning to make observations, even to someone who has never watched crickets before." The outcomes of

social interactions among crickets are generally unambiguous (Alexander, 1961).

The observers hierarchically ranked their subjective impressions of dominance status using a scale of 1 to 4 (1 being most dominant and 4 being least dominant) for each five minute block. Crickets that were determined to have similar dominance rank were given half-values: 1.5, 2.5, or 3.5, depending on their shared rank position.

Psychometric tests were performed to test (1) the temporal stability and interrater reliability of the subjective dominance ranks; (2) the inter-item consistency, temporal stability, and interrater reliability of the observed behavioral factors (AGGRESSION and SUBMISSION); and (3) the construct validity of subjective dominance ranks based on the observed behavioral factors. The findings of these psychometric tests are reported in the Results section. Based on the psychometric results indicating temporal stability, interrater reliability, and construct validity of the subjective dominance ranks, the subjective ranks for the stable dominance period (blocks 4-6) were aggregated into their *mean* (MSD) and standard deviation (SSD). MSD and SSD served as the rectilinear hierarchical model of dominance structure, since both were based on the methodologically imposed interval rating system of the observers. The two other possible dominance structures were created (based on theoretical concerns discussed in the Introduction):

despotic and curvilinear (logarithmic). Despotic dominance ranks (DSD) were obtained by assigning a nominal value of 1 to the top-ranking individual (rank 1) for each block of stable dominance section. All other ranks (ranks 2-4) were assigned a value of zero. These despotic scores were averaged over the stable dominance blocks, yielding the total percentage of time an individual male was despotic. Curvilinearity (LNMSD) was introduced into the model by performing a natural logarithmic transformation of MSD. All three structures of dominance were tested for their explanatory potential of the observed behavior scores.

Phenotypic measures of physical and behavioral traits.

The morphological measures were of the cricket bodies after death and the ages of the crickets throughout the study. Wet weights (WWGT) and dry weights (DWGT) were measured to an accuracy of 0.001 mg. Cuticular color was divided into three color types: dark (D), medium (M), and light (L). Color was initially rated at euthanization or at the death of a cricket. Color was rated again at the end of the study by two other independent observers. The color ratings were then converted into a numerical scale: D = -1; M = 0; L = 1. The reliability of the color ratings between raters was high, $r = 0.98$ (N = 100).

Assessment of the physical condition of the males consisted of assessing the intactness of body parts of the

males. Right and left antennae (RA, LA), right and left cerci (RC, LC) and the three right and left legs (RL1, RL2, RL3 and LL1, LL2, LL3) were assessed using a rank order scale: 0 = appendage missing entirely, 1 = 1/4 of appendage intact, 2 = 1/2 of appendage intact, 3 = 3/4 of appendage intact, and 4 = whole appendage intact. The possession and physical condition of the vestigial underwings and wings were assessed using a rank order scale: 0 = wing missing, 1 = highly irregular, 2 = moderately irregular, 3 = slightly irregular, and 4 = no irregularities. Irregularities of the wings and underwings were determined by assessing imperfections, such as the crinkled, torn, frayed or lopsided appearance of the wing. Untorn, unwrinkled and even wings and underwings indicated good condition.

Measures of bilateral asymmetry were computed by taking the absolute value of the difference between the ratings of the two corresponding appendages (e.g., difference between the two antennae [DA] = $|LA - RA|$). This difference score provided a quantitative value for how dissimilar or asymmetric two corresponding appendages were. High values indicated that the two appendages were very asymmetric, low values indicated symmetry. Measures of quality, defined in this study as body intactness, were computed by summing the two corresponding appendages (e.g., summation of both antennae [SA] = $LA + RA$). This summed score provided a quantitative value for how intact a cricket was at time of

euthanization. High values indicated an intact body, free of bodily injury; low values indicated broken appendages and substantial bodily injury. The cerci (SC, DC) and leg (SLL3, DLL3) scores were also obtained. The age of the crickets for each recorded song and during their stay in the competitive arena were assessed as number of days elapsed from the date of final molt to the date of the measured event. Attrition rate of the crickets was determined by calculating the number of crickets which died any time after or during the competitive interaction, and before completing all post-competitive recording sessions.

Those behavioral characteristics associated with the males' singing activities were measured during the audio-recording sessions. Singing time for each recorded song was measured in quarter hours from the time the lights went off to the time the song was recorded. Attempts was the number of times a cricket was placed in the sound chamber "without singing" and before an audio recording was obtained. If a cricket sang on its first time placed in the sound chamber, it scored a zero attempts. The variable attempts was assumed to be a motivational factor, measuring male proclivity to sing. Singing activity was determined by calculating the number of songs sung after the dominance interactions (PC songs).

Sonographic measures of calling song characteristics.

The male cricket calling songs were translated into a IBM-compatible 386 computer using an APAC Sound Blaster soundcard. The songs were analyzed using CSpeech Version 4 - Laboratory Automation Sound Analysis Software (P. Milenkovic, 1992) which measured and analyzed the song parameters. All song strings (a duration of audio recorded sound input) were passed through a 20 hertz high-pass filter to remove any low background sound components from the inputted sound string. Ten chirp periods were selected from each song string for each section of the experiment for each cricket. Ten song parameters were measured, as identified by Bennet-Clark (1989), which fell into two categories: between-chirp and within-chirp song parameters. To briefly review, cricket calling songs are composed of chirps, which in house crickets are delivered at fairly irregular intervals (see Appendix A for terminology). Each chirp is composed of syllables (usually three for house crickets). Based on these song structures, cricket songs can be quantitatively described at the chirp level or at the syllable level (syllables are within chirps). Measures that are only obtainable at the chirp level of analysis are the between-chirp parameters [e.g., the interval between two chirps cannot be described by syllable measures]. There were five between-chirp measures which are as follows: (1) chirp duration (CHL), (2) syllable

number (SYLN), (3) minimum frequency of the chirp (FMIN), (4) maximum frequency of the chirp (FMAX), and (5) interchirp interval (ICHL). Measures that are obtainable at the syllable level of analysis [e.g., syllable duration] are the within-chirp song parameters. There were five within-chirp measures which are as follows: (1) syllable duration (SYLL), (2) mean frequency of the syllable (FREQ), (3) sound intensity carried by the mean frequency (FREQI), (4) total sound intensity carried by all frequencies in the syllable (SYLI), and (5) intersyllable interval (ISL). All song duration parameters were measured in milliseconds. There were four song duration parameters measured, CHL, ICHL, SYLL, and ISL (as specified above). All frequency parameters were measured in Hertz. There were three frequency parameter measured, (1) the mean frequency of each syllable (FREQ), and (2) the minimum (FMIN) and (3) maximum (FMAX) frequency of each chirp (as specified above). The FREQ was measured as the principal frequency component from Fourier analysis found in each syllable. The FMIN and FMAX were obtained by measuring the low and high frequency components of a Time/Frequency Spectrogram derived for each chirp. All intensity parameters were measured in decibels relative to 1.75 volts RMS. The intensity values were converted from decibels into kvolts using decibel formula:

$$I = I_{\text{ref}} * 10^{(\text{db}/10)}$$

Two intensity parameters were measured: (1) the intensity of the mean frequency (FREQI), and (2) the intensity of the entire syllable (SYLI). The FREQI was measured in decibels taken from the Fourier analysis. An intensity difference (INDIFF) parameter was computed by subtracting the FREQI from SYLI: $INTDIFF = SYLI - FREQI$. Syllables consist of several component frequencies, however, the mean frequency usually carries most of the sound energy (intensity). The INDIFF parameter is a measure of the sound energy in frequencies other than the mean. If the mean frequency carried most of the sound intensity, then INDIFF would be zero (or negative due to estimation errors occurring during the Fourier analysis). If the other component frequencies carried a substantial amount of energy, then the intensity difference would be greater than zero.

Measurement Model Statistical Analyses

Data management. The subjective dominance ranks and observed behavioral factors data were organized within EXCEL® (Microsoft Inc., 1995). Observed behavior scores were based on the total occurrence of each of the behaviors within a block (quantitative ethogram). The subjective dominance ranks (MSD) and the observed behavior scores were divided into four data sets: (1) subjective dominance ranks for all crickets (rated by the primary observer); (2) subjective dominance ranks for the eleven groups rated by two

independent observers (the primary and a secondary); (3) observed behavior scores for all crickets, (rated by the primary observer); and (4) observed behavior scores for the eleven groups rated by two independent raters (the primary and one secondary). These data sets were translated into SAS-readable files and downloaded onto a VAX/VMS system using EpiInfo Version 6 (USDA).

The song characteristics data and physical data were organized within Statistica (StatSoft Inc., 1990). The physical measures were modified (as described below) within Statistica. Following this, the data sets were then translated into SAS-readable files downloaded onto a VAX/VMS system (using EpiInfo 6). All subsequent statistical analyses were performed with SAS statistic software (SAS, 1990). Several statistical procedures within SAS were used to aggregate, compose, and analyze the data: PROC CORR, PROC FACTOR, PROC GLM, PROC MEANS, PROC REG, PROC STANDARD, and PROC VARCOMP.

Psychometric analyses of social dominance. A generalizability theory (GT) approach was utilized as the primary psychometric tool to examine the construct validity, temporal stability, and interrater reliability of the dominance-related behavioral traits. Classical test theory (CT) results were provided for comparison with the GT

results. "Classical Test Theory defines reliability as the proportion of total variance which is true score variance" (Figueredo et al., 1992, pp. 421). Thus, CT only divides the total variance into two simple variance components: true score variance and error variance. CT ascribes the true score variance to continuity between observers (i.e., reliability). The error variance in CT is ascribed to the differences between observers' scores. CT does not allow for ascertaining the variances of the specific "effects" to be evaluated. Error variance contains multiple components of variance, rater variance being one of those elements. CT results do not allow for explicating whether the true score variance is due to temporal stability of the dominance ranks or due to interrater reliability. These two facets of the true score variance are lumped together as a whole. The same can be said of the error variance which again may be due to either to rater difference or to temporal differences. GT theory, in contrast, allows the true score and error variances to be further divided into more specific variance components, called "facets" (Figueredo, et al., 1992). GT allows for the evaluation of the many facets of the variance scores, including interaction terms such as Factor*Cricket which measures the individual differences in the factor scores of the crickets. GT analysis can allow for determination as to whether the error variance is

attributable to changes of the Subjects score due to temporal factors or due to observer differences. For the psychometric analyses of this study, both the CT and GT results were provided. For the purpose of this study, knowing the true variance component of each effect is preferred, so that the aspects of temporal stability, interrater reliability and inter-item consistency of subjective and observed measures of dominance could be assessed. For a more detailed discussion of generalizability theory and its uses see Figueredo, et al. (1995). Generalizability (GT) coefficients were obtained using the following equation, described in Figueredo, et al. (1995):

$$E^2_{rel} = \sigma^2_f / (\sigma^2_f + \sigma^2_{rel*})$$

$$* \text{ if } r \text{ is nested within } f: \quad \sigma^2_{rel*} = \sigma^2_{r(f)}$$

$$* \text{ if } r \text{ is crossed within } f: \quad \sigma^2_{rel*} = \sigma^2_{r*f}$$

The subjective dominance ranks (MSD) for the unlabeled (called blank) crickets were used for the psychometric analyses. Crickets were labeled randomly, so that the distribution of crickets that were unlabeled (i.e., blank) characterizes a representative sample of all the crickets. Both the subjective ranks and the observed behavior scores, from the data set containing the two observer ratings, were converted into z-scores (using PROC STANDARD), as specified by Figueredo et al. (1995). These data were differentiated into the two dominance periods of the videotapes: Formation and Stable dominance by creating a variable called Stable.

On the variable Stable, the Formation period was assigned a value of zero, and the Stable period a value of one.

A hierarchical general linear model was constructed to derive statistically independent variance components of the subjective dominance ranks (using PROC GLM Type I SS). Dominance group was not included in this analysis since the focal effects were the stability of each individual cricket's subjective ranks over blocks (time) and over raters. Estimated variance components for the elements of subjective rank were generated using PROC VARCOMP (see Appendix C). The following sequential order of components was rationally-derived for entering the crossed variables into the GT equation (pp. 122):

CRICKETS	9
BLOCKS	3
RATERS	2

The estimated variance components for each main element were converted into generalizability coefficients.

Two behavioral factors were created *a priori*, AGGRESSION and SUBMISSION, using the pre-specified behaviors of the quantitative ethogram (see Table 1, pp. 110) (using PROC FACTOR) for the unlabeled cricket. A hierarchical general linear model was constructed to derive statistically independent variance components of these observed behavioral factors (using PROC GLM Type I SS). The following sequential order was rationally-derived for entering the crossed

variables into the GT equation (pp. 122):

FACTORS	1
BEHAVIORS	16
GROUPS	7
CRICKETS	24
BLOCKS	2
RATERS	2

The interaction of crickets with factors (CRICKET*FACTOR) represents individual differences between the crickets in factor scores (i.e., different degrees of aggression and submission of individual crickets) and was the primary effect of interest in this portion of the study. Other focal effects evaluated in this study were the inter-item consistency of the factors based on the their component behaviors; and the stability of individual cricket factor scores over blocks and over raters. Estimated variance components for the elements of objective behavior scores and factors were generated using PROC VARCOMP. The estimated variance components of each main facets were converted into generalizability coefficients (using the GT formula, pp. 122).

A hierarchical general linear model (using PROC GLM) was run to analyze the correspondence between MSD and the observed behavioral factors for the unlabeled crickets. Subsequently, factors scores for AGGRESSION and SUBMISSION for all the crickets were determined (using PROC FACTOR).

Two final psychometric analyses, using all the crickets' data from the primary observer, were performed to test the correspondence between the observed behavioral factors and the three theoretically-specified structures of the subjective dominance ranks (despotism, curvilinear order, and rectilinear order) to determine which structure of dominance most closely characterized the observed behavioral factors.

(1) Correlations between the subjective dominance structures and the observed behavioral factors were obtained using PROC CORR. (2) A hierarchical general linear model (using PROC GLM) was run using a rationally-derived order for the three dominance structures: descending from the simplest dominance structure of despotism to the more complex structures of curvilinear order and rectilinear order, respectively. Although, curvilinear order is a more complex mathematical function than rectilinear order; and as specified by methodologists (Cohen & Cohen, 1983) should be entered into multiple regressions models following the rectilinear function. As a social structure a curvilinear function form is intermediate between despotism and rectilinear structures; for this reason, the curvilinear function form was entered into the GLM before the rectilinear function form.

A hierarchical general linear model (using PROC GLM) was run to analyze the effect of dominance rank on post-competitive attrition rates and singing activity.

Individual Differences in Male Phenotypic Traits.

Morphological measures were aggregated into cumulative physical variables (using PROC MEANS): quality means (QUALMEAN; i.e. body intactness), asymmetry means (ASYMMEAN), and color type means (COLOMEAN). QUALMEAN was the composite mean of all of the sums of the appendages (SA, SC, SLL3). ASYMMEAN was the composite mean of all of the differences of the appendages (DA, DC, DLL3). COLOMEAN was the composite mean of the three independent ratings of color type. ATTEMTEM was the mean number of attempts for each individual cricket over all his recorded songs. A correlation analysis was performed (using PROC CORR) to validate the correspondence between each mean composites and their component parts. All mean composites were highly correlated ($r = .47 - .93$, $p < .03$) to their component parts. Based on these results, all component parts were dropped as independent variables, and the composite means were used to characterize the physical traits.

Correlational analyses (using PROC CORR) were run to determine intercorrelations between the physical traits. Membership in a particular competitive group was tested to determine if the composition of the groups had an effect on the achieved dominance ranks; and to determine if dry weight and age had an effect on the achieved dominance ranks.

Song Characteristics Models. The songs of each cricket consist of two types of song components (see Appendix A, pp. 216): between-chirp and within-chirp components. The between-chirp components are those song components that are characterized by the measures on the individual chirps of a song: chirp duration, interchirp duration, minimum and maximum frequencies, and syllable number. The within-chirp components are those song components that are characterized by the measures on the individual syllables within a chirp: syllable duration, intersyllable duration, mean frequency, mean frequency intensity, total syllable intensity, and intensity difference between the total and frequency intensities.

A general linear model (PROC GLM Type I SS) was constructed to hierarchically derive independent variance components for the between-chirp song parameters. The following hierarchical sequential order was rationally-derived for entering the three nested levels of the song characteristics into the GT nested equation (pp. 122):

CRICKETS	43
SONGS (CRICKETS)	68
CHIRPS (SONGS)	929

For each between-chirp variable, the chirps within-songs facet was used as the error term to determine the appropriate F-value. Estimated variance components for each level of the

song characteristics for the between-chirp song parameters were generated using PROC VARCOMP. The estimated variance components of each facet were converted into generalizability coefficients (using the GT formula, pp. 122).

A hierarchical general linear model (PROC GLM Type I SS) was constructed to derive statistically independent variance components of the within-chirp song parameters. The following sequential order was rationally-derived for entering the four nested levels of the song characteristics into the GT nested equation (pp. 122):

CRICKETS	45
SONGS (CRICKETS)	71
CHIRPS (SONGS)	925
SYLLABLES (CHIRPS)	1806

For each within-chirp variable, the syllable within-chirps variance was used as the error term to determine the appropriate F-value. Estimated variance components for the levels of the song characteristics for the within-chirp song parameters were generated using PROC VARCOMP. The estimated variance components of each within-chirp song parameter were converted into generalizability coefficients (using the GT formula, pp. 122).

Based on the results the of these analyses, the individual song parameter measures were aggregated. Syllable (within-chirp) measures were aggregated by averaging over chirps, and the between-chirp measures aggregated by

averaging over songs within-cricket (using PROC MEANS). Two aggregated song parameters were obtained by averaging: the mean and the variance (σ^2) of the aggregates (component parts), such that a new data set was created which contained only the aggregated song components at the levels of between songs within-cricket and between crickets.

An orthogonal factor analysis (using PROC FACTOR Type VARIMAX) was used on the aggregated song components to identify common factors within songs, and to generate factor loadings. The use of common factors reduces the number of variables used in the model and enhances reliability by having a pooled measurements. Based on the results of the factor analysis (reported in the Results), the song characteristics factors were divided into the two experimental conditions, isolated-male (IM) and post-competitive (PC). The song characteristics factors were then subsequently pooled together within each condition and factor loadings obtained (using PROC FACTOR, TYPE VARIMAX.) These song characteristics factors and factor loadings were then exported to a new data file for structural analysis

Predictive Structural Modeling of the Isolated-male and Post-competitive Song Characteristics

A hierarchical general linear model (using PROC GLM) was constructed to determine the relationship between the song

characteristics and the crickets' behavioral and physical attributes within both experimental conditions.

In the Isolated-male condition, the physical traits measures were hierarchically entered as predictors of the song characteristics factors. First, the between-cricket physical traits measures (singular one-time measures) of size, quality, asymmetry, color were entered, followed by the within-cricket physical traits measures (repeated longitudinal measures) of age, time , and attempts. Standardized regression coefficients (PROC REG) were obtained for the variables which were significant predictors of the song characteristics factors, to determine strength and direction of their relationship.

In the Post-competitive condition, the behavioral and physical traits measures were hierarchically entered as predictors of the song characteristics factors. First the behavioral properties of the competitive interactions were entered, the three hypothetical structures of dominance order, and the AGGRESSION and SUBMISSION factors; followed by the between-cricket physical traits, and their interactions with the behavioral measures; and lastly the within-cricket physical traits measures. Standardized regression coefficients for the variables which were significant predictors of the song characteristics factors were obtained to determine strength and direction of their relationship (using PROC REG).

RESULTS

Social Dominance in Male House Crickets

Psychometrics of the Subjective Dominance Ranks

Overall the CT reliabilities for "true score" variance of the subjective dominance ranks were relatively high for both the formation and stable dominance periods, $r = .733$ and $r = .934$, respectively. The CT results also indicated that the dominance ranks were more variable over the formation period than the stable period. This was anticipated, because during the formation period, the males were at their initial stages of agonistic encounters, and only beginning to gauge the other's physical and motivational attributes. These CT reliabilities, however, were unable to specifically discriminate between the effects of interobserver error or temporal differences in the observed dominance ranks. The intent of these analyses was to determine if the dominance ranks were a "real" property of the individual crickets. The question was, therefore: were the observed dominance ranks stable over time and over the observers? Generalizability coefficients use the separate variance component of each specific "facet" effect, this allows for differentiation between temporal effects and observer effects. Using the estimated variance components

(estimated using VARCOMP provided in Appendix C, Table C.2), the GT coefficients were obtained as follows:

<u>FACET</u>	<u>E²_{rel} Formation</u>	<u>E²_{rel} Stable</u>
Blocks	.993	.988
Raters	.987	.994

The E²_{rel} over blocks indicates strong temporal stability of the subjective dominance ranks over the blocks within both dominance periods. Based on the GT coefficients, the difference in temporal stabilities of the ranks between the two periods is negligible. The E²_{rel} over raters indicates high reliability between the two independent observers for each group. These results indicate that the dominance ranks remained relatively stable over time and across raters, providing evidence that the measured rank differences between crickets were due to "real" behavioral attributes of the crickets. Based on the reliable temporal stabilities of the dominance ranks over blocks, the ranks for the stable period were pooled into a mean subjective dominance rank factor. The formation period ranks were dropped, because the desired data for the predictive analyses was the final established dominance outcome.

Psychometrics of the Observed Behavioral Factors: AGGRESSION and SUBMISSION

The observed behavioral items from the quantitative ethogram were *a priori* placed into two behavioral factors

(see Table 1): AGGRESSION and SUBMISSION. These factors were then psychometrically evaluated for inter-item consistency (did the crickets' factor scores account for the variance in the behavior items scores?), temporal stability (did the crickets' factor scores remain consistent over time?), and interobserver reliability (were the crickets' factor scores consistent over observers?). The estimates of CT reliability for the "true score" variance of the observed behavioral factors were $r = .681$ and $r = .532$ for the formation and stable periods, respectively. Again, the CT reliabilities were respectable overall for measures of latent behavioral factors. These scores were smaller in magnitude than the scores for the subjective ranks. According to CT theory, this implies low interrater reliability; however, as stated before, CT is unable to determine the specific "effects" variances within the true score or error variances. The GT results listed below indicate that the decreased magnitude of the true score variance is due to the degree of factor specification (common variance between the items and their latent factor) and is not due to observer effects. The Generalizability coefficients constructed from the estimated variance components (using VARCOMP provided in Appendix C, Table C.4) were as follows:

<u>FACET</u>	<u>E²_{rel} Formation</u>	<u>E²_{rel} Stable</u>
Behaviors	.550	.548
Blocks	.997	1.000
Raters	1.000	1.000

The E^2_{rel} over behaviors indicated the inter-item consistency of the observed behavioral factors to their constituent behavior items (the individually scored behaviors of the ethogram). These GT coefficients indicated how well the behavior items fitted together as a latent behavioral factor. Although, not overwhelming high, the inter-item consistency of the behavioral factors verified the construct validity of the factors for explaining the agonistic behavior patterns of the crickets. Although, Generalizability theorists tend to avoid specifying absolute cut-offs, a GT coefficient of 0.5 or higher for items on a scale (e.g., factor loadings) is usually considered respectable (A. J. Figueredo, personal communication). The correspondence between these cricket behaviors and their factors are acceptable in psychometric terms (Figueredo et al., 1995). These were fairly good latent factor scores, since the behavior items in each factor may serve alternative functions not specified by the factor per se. The aggressive and submissive functions of a behavior may only be one portion of a behavior's full functional repertoire. For example, the behavior *approaches* can be aggressive, incidental or investigative in nature.

These results demonstrated how well *approaches* fits with other behavioral items that are defined as aggression. The E^2_{rel} over blocks and raters were high, indicating consistent temporal stability and interrater reliability of the behavioral factors. The E^2_{rel} over blocks indicates strong temporal stability of the behavioral factors over the blocks within each dominance period. The E^2_{rel} over raters indicates high interobserver reliability for the behavioral factors. The lower magnitude of the CT reliabilities for the behavioral factors was due to the reduced factors' inter-item consistency and not due to temporal or observer effects. These results supported the assertion that the specified latent behavioral factors characterized the patterns of agonistic behaviors exhibited by the competitive interactions of the individual crickets in their groups; and that these behavioral factors were persist over time and not due to observer differences.

The CT reliabilities between the Formation and Stable periods revealed what was an unanticipated decline ($r = .681$ to $.532$, respectively). The expectation was that the stabilized dominance hierarchies of the Stable period would produce more consistency in the behavioral factor scores of the individual crickets than would the more transient hierarchies occurring during the Formation period. However, a secondary examination of the ethogram data revealed a steep

decline in the gross numbers of behavior occurrences in the Stable period. Once a stable dominance hierarchy is established, less overt aggression is necessary to maintain the dominance order, then is necessary to obtain it. Based on this characterization of stable dominance, the crickets would be expected to interact less often in the Stable period, such that fewer individual agonistic behaviors would be observed. This was in fact what happened; in several blocks of the Stable period no agonistic behaviors occurred. This reduced the numbers of quantitative estimates and, therefore, the power of the statistical analyses. The result was lower true score variance estimates. Ethologically, the lower numbers of behavioral occurrences was expected, however, for quantitative analyses the lower numbers reduced statistical values.

Subjective Dominance Rank as an Index of The Observed Behavioral Factors: AGGRESSION and SUBMISSION

The hierarchical general linear model regressing the observed behavioral factors on their subjectively determined dominance ranks resulted in the F-ratios and R^2 -values reported in Table 2. The F-values for the observed behavioral factors were derived by using the Factor*Cricket variance (the individual differences in factor scores of the crickets) as the error term.

Table 2

Predictive Validity Between Subjective Dominance Rank and the Observed Behavioral Factors: AGGRESSION and SUBMISSION

Behavioral Factors	df	F	sR ²	sR
		Subjective Dominance Rank		
AGGRESSION	1	42.66*	.31	.56
SUBMISSION	1	104.07*	.25	.50

Note. Factor*Cricket indicated the individual differences in scores on each factor and was used as the error term to test the significance of subjective dominance rank. *P(Ho) < .05.

The subjectively determined dominance ranks were able to characterize the individual differences in the behavioral factors. The observed subjective dominance ranks provided useful indices of the behavioral factors: AGGRESSION and SUBMISSION over crickets and blocks. This supports the assertion that the agonistic behavior patterns in groups of crickets are easily recognizable by human observers and characterized as subjectively rated dominance ranks.

In conclusion, the psychometric analyses of social dominance in crickets presented here supported the assertion that dominance ranks were (1) "real" traits of the individual crickets behavior, and (2) characteristic of the individual differences in the observed behavioral factor scores, which in turn, explained the patterns of agonistic behavior in the

crickets. In addition, the subjective dominance ranks and the observed behavioral factors were due to differences among the observers: over crickets, dominance periods, or blocks. From this point on, further analyses were conducted under the assumption that dominance relationships among the crickets readily accounted for the agonistic behavior patterns and that the dominance "rank" of the males were tangible aspects of the males' phenotypic profiles.

Structure of the Social Dominance Orders

Before conducting analyses on the intrinsic structure of the crickets' dominance relationships, it was first necessary to determine if the group to which a cricket was a member affected that cricket's rank or agonistic behavior patterns. For example, a large or highly aggressive cricket could have been placed in a group with three relatively small or less aggressive crickets. This situation would potentially bias the larger or more aggressive cricket to obtain a higher group rank than if it had equally matched rivals. For this reason, the dominance ranks and behavioral factors had to be analyzed for group effects, which could be statistically controlled for. Membership in a particular dominance group had no effect on the crickets' observed subjective ranks (MSD) ($F(75,24) = 0.04$, n.s.), but group did have an effect on the variability in the observed ranks (SSD) ($F(75,24) = 5.4$, $p < 0.05$). Group membership affected the SUBMISSION

factor scores ($F(72,23) = 4.83, p < 0.05$) but not the AGGRESSION factor scores ($F(72,23) = 1.5, n.s.$). The effects of group membership on rank variability and the SUBMISSION factor scores were statistically controlled for by regressing group variance effects out of the observed ranks (MSD), and the two behavioral factors (AGGRESSION and SUBMISSION).

The structure of the dominance order in the crickets was evaluated by generating correlations between the three hypothesized structures of dominance: despotism, curvilinear rank, and rectilinear rank by the behavioral factors. Despotism was generated by determining the top-ranked cricket and assigning that cricket a value of 1; all lower-ranking crickets were assigned a value of zero. The observed subjective dominance ranks (MSD) were methodologically specified as being rectilinear: having equivalent intervals between the ranks. In order to generate one structural scale intermediate between despotism and rectilinear rank, a natural logarithmic transformation was applied to the observed ranks (MSD). This logarithmic "curvilinear" scale created larger intervals between the higher ranks (e.g., ranks 1 and 2) than between the lower ranks (e.g., ranks 3 and 4: see Figure 1). Because a curvilinear scale is mathematically more complex, it is usually entered into general linear model procedures after the rectilinear scales (Cohen & Cohen, 1983). In terms of complexity of social structures, the curvilinear function was intermediate between

despotism and rectilinear functions. For this reason, the curvilinear (natural logarithmic) function was entered into the general linear models procedure before the rectilinear function. Additionally, it should be noted that in despotism the depot is assigned a higher numerical value (1) than the subordinates (0); this is not true for the two linear structures, in which the lower-ranking crickets are assigned higher numerical values with decreasing rank, this reverses the sign of the correlations between despotism and the linear ranks.

The correlations between the behavioral factors (AGGRESSION and SUBMISSION) and the three structures of dominance, despotism, curvilinear rank and rectilinear rank were given in Table 3.

Table 3

Correlation Coefficients for the Dominance Structures

Dominance Structures	N	r	
		Aggression	Submission
Despotism (1,226)	230	.70*	-.48*
Curvilinear (1,226)	230	-.77*	.47*
Rectilinear(1,226)	230	-.76*	.44*

Note. * All were significant $P(H_0) < .0001$.

All three dominance structures were significantly correlated to both the AGGRESSION and SUBMISSION factors. The general results for all structures indicated that higher-ranking crickets were more aggressive and less submissive than the lower-ranking crickets. Lower-ranking crickets were more submissive and less aggressive. These correlations did not rule out any of the three dominance structures, since all three structures showed nearly equivalent correlations. Despotism, curvilinear rank, and rectilinear rank were hierarchically-placed into a general linear models procedure, and resulted in the following F-ratios found on Table 4.

Table 4

General Linear Model for the Dominance Structures

Dominance Structures	<u>df</u>	F	
		Aggression	Submission
Despotism	1	282.91*	69.91*
Curvilinear	1	72.21*	4.92*
Rectilinear	1	3.94*	0.07
<u>R</u> ² (Model)		(0.61)	(0.25)

Note. N = 230. *P(Ho) < .05. Values in parentheses are R².

These F-ratios indicated that AGGRESSION was best characterized by the rectilinear dominance structure since the despotic and curvilinear functions could not adequately

account for all the variance in the aggression factor scores. Rectilinear dominance continued to be significantly related to AGGRESSION after two socially less complex dominance structures' variance was removed. This result indicated that the AGGRESSION factor scores had equidistant intervals between the ranks. The amount of aggressive behaviors declined equally by rank, such that each rank in the dominance hierarchy indicated the amount of aggression each cricket displayed toward the other crickets with descending rank. The SUBMISSION factor scores were characterized by a curvilinear dominance structure; all variance in the SUBMISSION factor scores were explained by the curvilinear function. Lower-ranking individuals were far more submissive than the higher-ranking individuals. SUBMISSION scores did not decrease gradually with rank as a rectilinear configuration would imply, but drop off dramatically as rank increases. This implied two behavioral patterns: (1) higher-ranking males were not submitting as readily to aggression as were lower-ranking males, and (2) lower-ranking males were submitting without being aggressed upon (i.e. occurring without correspondence to aggressive behaviors), implying that submissive behaviors may be functioning in other behavioral contexts. As the squared multiple correlation indicated (Table 4, line 4), the amount of variance in the SUBMISSION factor ($R^2 = .25$) explained by dominance order was much smaller than AGGRESSION ($R^2 = .61$),

implying that submissive behaviors were less characteristic of the dominance orders than were the aggressive behaviors. This result suggested that submissive behaviors (SUBMISSION) were functioning in other domains other than dominance relationships. Despotism, as a structure of the crickets' dominance relationships did not adequately explain either the AGGRESSION or SUBMISSION factor, suggesting that it was not an adequate representation of dominance in the crickets. The results of these two analyses indicated that dominance order in the crickets was in fact a linear hierarchy. The crickets were differentially aggressive and submissive based on their dominance rank. Rectilinear dominance ranks were, therefore, meaningful and quantitative indices of the aggressive behavior patterns of the male crickets, as observed by Alexander (1961). This study also indicated that curvilinear dominance ranks were indicative of submissive behavior: the interval amounts of the submissive behaviors were not equivalent based on rank.

Because a great deal of the variance (Table 4, line 4) in the AGGRESSION and SUBMISSION behavioral factors remained unaccounted for by the dominance structures, the behavioral factors were retained for the later analyses as independent behavioral traits, in addition, to the dominance structures. In this way, potential phenotypic variances characteristic of the behavioral factors, but unspecified by dominance, could be analyzed as potential song characteristic correlates in

conjunction with the other morphological and behavioral male attributes.

Physical Traits Potentiating Dominance Ranks

Several physical attributes were evaluated as potential effects in determining the crickets' dominance ranks. Two male attributes were specified by Alexander (1961) as potentially influencing the rank a cricket obtains: size and age. Alexander (1961) found that age but not size significantly affected the rank obtained by *G. integer*, with older males acquiring higher ranks. Cade (1979) found that neither size nor age affected *G. integer's* acquired dominance status. The results of these physical trait analyses indicated that in *A. domesticus* neither size nor age had any effect on the observed dominance ranks ($F(1,97) = 3.09$, & 0.17 , $p > .05$) or the behavioral factor scores (AGGRESSION ($F(1,93) = 0.19$, & 0.57 , $p > .05$) and SUBMISSION ($F(1,93) = 0.20$, & 0.65 , $p > .05$) of the males in this study. The observed dominance ranks and the behavioral factors were not correlated to any of the other measured phenotypic attributes of the crickets (asymmetry, quality, color, dryweight, drylength, or attempts).

Alternative Behavioral Responses in Subordinate Crickets

The intermale competitive interactions (i.e., the dominance groups) had a suppressive effect on singing

behavior and activity (i.e., the number of songs recorded post-competitively) in the lower ranking males. In addition, the competitive interactions were fatal to a number of the lower ranking crickets, leading to a higher attrition rate among the subordinate males after the competitive interactions. The mean number of songs sung based on rank after the intermale interactions are as follows:

<u>RANK</u>	<u>N</u>	<u>% Survivorship</u>	<u>Mean (PC) Songs</u>
1 - 1.5	25	100	1.80
2 - 2.5	35	91	1.45
3 - 3.5	23	83	1.25
4	18	77	0.88

The number of post-competitive songs sung was negatively correlated to dominance rank ($r = -0.37$, $p < .05$), indicating that several subordinate males ceased to sing after the intermale interactions. Cade (1979) found similar results, suggesting that the males were adopting alternative strategies. Cade suggested four alternative strategies, calling softly, calling before dawn, satellite behavior, and attacking calling males. In the behavioral observations of the dominance groups in this study, several different alternative behaviors to singing were observed. The most common spacing behavior observed by the raters was a group pattern coined by the observers in this study as "the four-corners." This group pattern appeared to be the crickets' attempts to achieve optimal spacing within the confines of

the competitive arena. The crickets would optimally space themselves in a square-like dimension along the walls of the circle. Another frequent group behavioral pattern was for one cricket to call loudly , usually the dominant cricket and usually from the water-sponge, while all the other crickets remained silent and spaced out. Rarely did more than one cricket call in the arena. Usually if another cricket other than the dominant started singing, that cricket would be attacked by the dominant one. Satellite behavior was a frequent occurrence in the groups: one silent cricket remained near the calling male. Another common behavior among the crickets was climbing the edges of the arena, in a seeming attempt to get out, in fact, one tenacious cricket managed to escape from the competitive arena during the study. In agreement with Alexander's (1961) observation of one male courting (i.e., singing courtship song) another, this behavior was documented on several occasions in this study. Usually a calling male is approached from behind by a male which acts passively (pseudofemale behavior?; a male usually threatens on an approach). The result is a male-to-male courtship, suggesting the possibility of pseudofemale behavior as an alternative male behavior strategy. Although no systematic analysis of these group behaviors was performed, these patterns arose frequently enough to warrant their discussion.

Attrition rate was positively correlated to dominance rank ($r = 0.27$, $p < .05$). Lower-ranking males were more likely to die and less likely to sing after dominance. Death and dominance rank were hierarchically modeled on the number of post-competitive songs, controlling for the event that death was the cause for failing to sing. Both death and rank were negatively correlated with the number of post-competitive songs ($\beta(90) = -0.35$; $\beta(90) = -0.25$, $p < .05$, respectively), which indicated that the competitive interaction caused a higher attrition rate and less post-competitive singing in lower ranking males.

Individual Differences Among Male House Crickets

Phenotypic Attribute Differences Between the Male Crickets

Intercorrelations were tested (using PROC CORR) between the morphological and behavioral traits measured for each individual cricket and are provided in Table 5. Intercorrelations were found between several of the physical characteristics (Table 5). ASYMMETRY and QUALMEAN were negatively correlated ($r = -0.58$, $p < .05$). QUALMEAN or body intactness and asymmetry (the differences between the body appendages) were linked: as body intactness decreased (more legs, cerci and antennae broken), the crickets' bodies also became less symmetrical.

Table 5

Physical Traits Intercorrelations

Physical Traits	ASYMMETRY	QUALMEAN	COLOR	ATTEMPTS	DWGT	DLG
ASYMMETRY	1.00	*	*	*	*	*
QUALMEAN	-0.58*	1.00	*	*	*	*
COLOR	-0.12	0.13	1.00	*	*	*
ATTEMPTS	-0.04	-0.06	0.06	1.00	*	*
DWGT	0.03	0.10	-0.09	-0.20*	1.00	*
DLG	0.24*	0	-0.04	-0.23*	0.75*	1.00

* $P(H_0) < 0.05$

This relationship indicated that injury to the body did not usually occur symmetrically. ASYMMETRY was positively correlated to DLG ($r = 0.24$, $p < .05$). Males with longer bodies were more likely to be asymmetrical. Both DWGT and DLG were negatively correlated with ATTEMPTM ($r = -0.20$; -0.23 , $p < .05$, respectively). ATTEMPTM may possibly be a motivation measure, since it is operationalized as "the number of times a male was placed in the sound chamber before he sang"; implying that males with fewer attempts were more inclined to sing. DWGT and DLG were measures of male size. Fewer attempts were needed in order to get an audio-recording of larger males, implying that large males were more motivated to sing. DWGT and DLG were highly correlated ($r = 0.75$, $p < .05$) since they were both related to male size.

Because of the high intercorrelation between DWGT and DLG, DLG was dropped from the rest of the analyses. Most studies in the field operationalize dryweight as the measure of male size. No other significant correlations were found between the physical factors.

Song Characteristics Differences Between the Male Crickets

Between and within song characteristics consistencies.

These results were originally presented in an earlier master's thesis (Sage, 1996), and were reproduced and expanded here to provide a foundation for understanding the subsequent results obtained for the doctoral thesis. To review, the between-chirp and within-chirp variables involved measures at different levels in the song characteristics. The between-chirp measures were those measures that were acquired from the chirp level, i. e., were singular measures from the chirp. The within-chirp measures were those measures acquired from the syllable level, i. e., several successive measures of the syllable components within the chirp. A hierarchical general linear model procedures (using PROC GLM) was applied to the between-chirp song components using three nested levels: cricket (the variance between different crickets), song within-cricket (the variances between the song bouts of individual crickets), and chirp within-song (the variance between the chirps within a song

bout); as predictors, and resulted in F-ratios provided on Table 6 (pp. 150). The chirps within-song variance served as the error term for the between-chirp song components. All the between-chirp song components varied significantly between crickets and between the song bouts within-crickets, indicating that the between-chirp elements of the crickets' songs were significantly different between the crickets, and were therefore individually characteristic of each cricket.

Table 6

F-ratios for Between-chirp Song Components

Song Levels	N	DF	F				
			CHL	SYLN	FMIN	FMAX	ICHL
Cricket	68	43	1.68*	2.10*	4.93*	2.97*	1.88*
Song(cricket)	929	68	2.88*	3.46*	1.79*	15.11*	8.38*

Note. Modified table taken from Sage (1996). *P(Ho) < 0.05

These findings also, indicated that individual song bouts were discrete, suggesting that the between-chirp song components change over singing occasion. These changes in the song characteristics could be caused by timing, age, development, male strategy, and situational effects during the occasion of a male's singing. The cricket (differences between crickets) and song within-cricket (differences

between the four recorded songs of each cricket) variables accounted for most of the variance in the between-chirp song components.

A generalizability analysis was performed on the between-chirp song components in order to determine generalizability of these components across each level of component variances. Estimated variance components for the between-chirp song components were attained (using PROC VARCOMP) for each of the three nested-levels: cricket, songs within-cricket, and chirps within-song (provided in Appendix D, Table D.1), which estimates and separates each elements variance components. Negative variance values were interpreted as zero, because negative variance estimates are artifacts of the estimation procedure occurring when the true values of the parameters are very close to zero (Figueredo et al., 1995). GT coefficients were calculated using the GT formula (pp. 122) to test the internal consistency of each between-chirp component for cricket and song within-cricket. These GT coefficients are comparable to reliability tests: they indicate whether the nested variable is a good or reliable measure of the variable they are nested within. At this point it might be helpful to review the interpretation of GT coefficients, using the two variance components generated for this analysis: cricket and song within-cricket for the between-chirp component, chirp duration (CHL). If the chirp duration differences between the crickets are small

(numerator variance), and the differences between the songs of each individual crickets are small (denominator variance) then this implies that chirp duration is a species-specific song characteristic, since it varies little between crickets and within individual crickets. If the chirp duration differences between the crickets are large, but the differences within a cricket are small, then this implies that chirp duration is specific to the individual (demonstrates individual differences in chirp duration). If the chirp duration difference between crickets is large and the differences within crickets are large, then this implies a highly variable chirp duration not highly characteristic of the species or the individual cricket. An example of this is the interchirp duration (ICHL) in house crickets, as Alexander (1961) characterized it as "irregularly delivered chirps." In correspondence with Alexander's suggestion, the interchirp duration (ICHL) GT coefficients (Table 7, column 6) were small, the result of large between-cricket variances (numerator) and large within-cricket variances (denominator) (Appendix D, Table D.2). This was also true of the small chirp duration (CHL) coefficients (Table 7, column 2). In addition to the chirp duration and the interchirp duration, the syllable number (SYLN) coefficients were also small. However in this case, the variances both within and between crickets were small, indicating that the syllable number was very species-specific.

Table 7
Generalizability Coefficients for Between-chirp Song Components

Song Levels	E^2_{rel}				
	CHL	SYLN	FMIN	FMAX	ICHL
Cricket	0.30	0.39	<u>0.78</u>	0.46	0.29
Song(cricket)	0.17	0.21	0.08	<u>0.60</u>	0.46

Note. This table is a modified version taken from Sage (1996), variance components are provided in Appendix D.

Highly generalizable within crickets was the minimum frequency (FMIN) of the chirps ($E^2_{rel} = 0.78$), indicating that the minimum frequency consistently differed between crickets and was highly characteristic of each individual cricket. The minimum frequency was individual for each cricket but did not differ substantially between each of the cricket's songs ($E^2_{rel} = 0.08$). The minimum frequency provided an individual's "signature" component of the male's calling song. The maximum frequency (FMAX) of the songs was highly variable between-crickets and between each cricket's songs as indicated by a low coefficient ($E^2_{rel} = 0.46$); however, the maximum frequency was consistent within song, indicating it was highly characteristic of the song bouts ($E^2_{rel} = 0.60$). The minimum and maximum frequency song parameters were retained as indicative of the individual male's song

characteristics for the correspondence between male song characteristics and male phenotype. Chirp duration, interchirp duration, and syllable number were not retained for song characteristics correspondence to individual male phenotype: chirp duration and interchirp duration were too variable to be indicative of male phenotype; and the syllable number was indicative of species and would not serve to indicate individual male phenotypic traits (Table 7).

Next, a hierarchical general linear model procedure (using PROC GLM) was applied to the within-chirp song components: syllable duration (SYLL), mean frequency (FREQ), mean frequency's intensity (FREQUI), total syllable intensity (SYLI), and intersyllable duration (ISL); using four nested levels: cricket, song within-cricket, chirp within-song, and syllable within-chirp (the variance between the syllable measures within a chirp) as predictors. The syllable within-chirp variance served as the error term for the song levels. This model resulted in the following F-ratios provided in Table 8. All the within-chirp song components (syllable measures) varied significantly between crickets. All the within-chirp song components varied significantly between the song within-cricket, except the syllable intensity (SYLI). All the within-chirp song components varied significantly between the chirps within-song, except the intersyllable duration (ISL).

Table 8

F-Ratios for Within-chirp Song Components

Song Levels	N	DF	F				
			SYLL	FREQ	FREQI	SYLI	ISYLL
Cricket	71	45	10.36*	10.25*	2.36*	1235.9*	3.15*
Song(cricket)	925	71	12.76*	3.97*	15.91*	0	3.29*
Chirp(song)	1806	925	1.16*	1.30*	2.13*	1.65*	0.80

Note. This table is a modified version taken from Sage (1996). *P(Ho) < .05.

The cricket and song variables accounted for most of the variance within the within-chirp song components; however, the chirps within a song did vary significantly on several song components.

A generalizability analysis was performed in order to determine if these within-chirp song components were generalizable within each level. Variance components were attained for each variable (using PROC VARCOMP) (are provided in Appendix D, Table D.2). Negative values were interpreted as zero (see explanation, pp. 151). GT coefficients (pp. 122) were computed for each within-chirp song component, testing the internal consistency of each variable over cricket, song within-cricket and chirp within-song, provided on Table 9. All the within-chirp components were

generalizable across either the cricket or song within-cricket levels.

Table 9

Generalizability Coefficients for Within-Chirp Song Components

Song Levels	E^2_{rel}				
	SYLL	FREQ	FREQI	SYLI	ISL
Cricket	<u>.80</u>	<u>.83</u>	.37	<u>1.0</u>	.54
Song(Cricket)	<u>.90</u>	.58	<u>.75</u>	0	<u>1.0</u>
Chirp(Song)	.06	.10	.30	0	0

Note. This table is a modified version taken from Sage (1996), variance components are provided in Appendix D.

The syllable duration (SYLL), mean frequency (FREQ), and the syllable intensity (SYLI) had large between cricket variances, but small within cricket variances. This indicated that crickets were substantially distinct from each other but were internally consistent. The intensity of the mean frequency (FREQI) was highly variable between each cricket's song bouts, resulting in a low between cricket GT coefficient ($E^2_{rel} = .37$); however, FREQI was internally consistent within a song bout; i. e., the differences between the chirps within a song were small ($E^2_{rel} = .75$). The intersyllable duration (ISL) between crickets resulted in a moderate GT coefficient ($E^2_{rel} = .54$). However, the variances

components indicated that the differences between crickets and between songs within the crickets were both large, i.e. not characteristic of individual crickets, since the song bout ISL's were not distinct. The intersyllable duration (ISL) was internally consistent within a song bout ($E^2_{rel} = 1.0$). The intensity difference measure (the SYLI minus FREQI, operationally defined pp. 119) was retained, since it incorporated the syllable intensity and the mean frequency intensity which were both retained following this analysis. Chirps within-song had low GT coefficients over all the syllable components (Table 9, line 3). None of the within-chirp song components were highly variable at the chirp level; variances between chirps within a song and between syllables within a chirp were both small. This result indicated that all the within-chirp song parameters were aggregatable across the chirps within songs. As was true for the between-chirp components, crickets and songs within-cricket served as the best predictors for the within-chirp song components' variabilities.

All of the within-chirp song components were retained and aggregated across chirps within-songs. The between-chirp song components, minimum frequency (FMIN) and maximum frequency (FMAX) were retained and aggregated across chirps within-songs. Since the song bouts within a cricket were significantly different from each other, songs were not aggregated within crickets. Both the between-chirp and

within-chirp components were collapsed (using PROC MEANS) across syllables and across chirps to create fourteen aggregated variables composed of the song components' *means* and *standard deviations*: (1) mean of syllable duration means (MSYLL), (2) mean of syllable durations standard deviations (MSYLSLSD), (3) mean of intersyllable duration means (MISL), (4) mean of intersyllable duration standard deviations (MISLSLSD), (5) mean of syllable intensity means (MINT), (6) mean of syllable intensity standard deviations (MINTSD), (7) mean of syllable frequency means (MFREQ), (8) mean of syllable frequency standard deviations (MFRQSD), (9) mean of syllable intensity differences means (MINTDF), (10) mean of syllable intensity differences standard deviations (MINTDFSD), (11) mean of frequency minimums (MFMIN), (12) mean of frequency maximums (MFMAX), (13) mean of interchirp durations (MICHL), and (14) mean of syllable number (MSYLN). These aggregated terms reduced the data set into four specific song categories from the experimental song conditions: (1) isolated-male song 1, (2) isolated-male song 2, (3) post-competitive song 1, and (4) post-competitive song 2.

Latent Common Factors of the Song Characteristics Differences

Factor Specification for the Aggregate Measures of the Song Characteristics

As discussed by Popov and Shuvalov (1977) and Thornhill and Alcock (1983), the song components may measure some general feature or construct of the song characteristics such as "frequency" or "intensity." Since all of the song component measures are composed of measures of frequency, intensity, and duration, it is highly probable that several of these measures are indicative of the same underlying dimensions of the song characteristics. For this reason, an exploratory factor analysis (using PROC FACTOR) was performed on each song category (four song recording events) to analyze the interrelationships among the fourteen aggregated variables; and to determine if there were underlying dimensions of the song characteristics that could account for these interrelationships among the variables. In all four of the song categories, the *MEAN* song variables were explained by two factors, and the *STD* (standard deviation) song variables by one factor. An interesting property of the factor loadings for these three song factors emerged when the isolated-male song categories' and post-competitive song categories' factor loadings were compared. Within each experimental condition (isolated-male and post-competitive), the song parameters grouped on to the same factor; however, between the two experimental conditions, song parameters grouped on to different factors. Table 10 is a sample listing of the factor loadings for the Mean factors of each song category and is provided to illustrate this result.

Table 10

Factor Loadings of the Song Components

Song Components	Song 1	Song 2	Song 3
<u>Isolated Males Mean Factor 1</u>			
MFREQ	0.94	0.91	0.94
MFMIN	0.81	0.61	0.48
MFMAX	0.68	0.72	0.94
MSYLL	-0.40	-0.32	-0.35
<u>Isolated Male Mean Factor 2</u>			
MINT	0.77	0.82	0.82
MINTDF	-0.51	-0.57	-0.46
<u>Post-competitive Mean Factor 1</u>			
MFREQ	0.79	0.86	0.0
MINT	0.79	0.52	0.0
MINTDF	-0.59	-0.56	0.0
MFMAX	0.77	0.80	0.0
<u>Post-competitive Mean Factor 2</u>			
MSYLL	0.75	0.71	0.0
MISL	-0.52	-0.65	0.0
MFMIN	0.57	0.59	0.0
MSYLN	0.49	0.47	0.0

Note. This table is taken from Sage (1996).

The implication of these results was that differences between the song bouts of the crickets (Tables 6-9) were caused by differences in the songs between the two experimental conditions, i.e. the effect of the competitive interaction. Guided by this property of the song factors, all the isolated-male song parameter measures and all the post-competitive song parameter measures were pooled together within their song condition, making two general song factor categories: isolated-male and post-competitive. The three song factors were specified within both the isolated-male and post-competitive conditions: two factors accounted for the parameter aggregates of the means and the one factor accounted for the parameter aggregates of the standard deviation. The song factors were characterized by different song parameters between the isolated-male and the post-competitive song conditions.

Isolated-male Song Characteristics Factors

An orthogonal factor analysis (using VARIMAX) constructed the following factors and factor loadings for the isolated-male condition provided on Table 11 (pp. 162). The Isolated-male *Mean* factors clearly involved frequency (IM Mean Factor 1) and intensity (IM Mean Factor 2) differences between the crickets. The Isolated-male FREQUENCY factor was represented by the song parameters of the frequency envelope, in that it encompassed the intercorrelations between the

Table 11

Isolated Male Calling Song Factors And Factor Loadings

Song Components	Mean Factor 1	Mean Factor 2
Mean Syllable Duration	-0.373	0.385
Mean Intersyllable Duration	0.040	-0.262
Mean Intensity	-0.007	<u>0.799</u>
Mean Frequency	<u>0.928</u>	-0.022
Mean Intensity Difference	-0.287	<u>-0.573</u>
Mean Min. Frequency	<u>0.695</u>	-0.113
Mean Max. Frequency	<u>0.719</u>	0.068
Mean Interchirp Duration	-0.051	0.072
Mean Syllable Number	-0.105	0.103
Standard Deviation Factor		
Syllable Duration SD	0.082	
Intersyllable Duration SD	0.083	
Mean Intensity SD	<u>0.934</u>	
Mean Frequency SD	-0.060	
Mean Intensity Difference SD	<u>0.926</u>	
Mean Min. Frequency SD	-0.076	
Mean Max. Frequency SD	-0.094	
Mean Interchirp Duration SD	0.131	
Mean Syllable Number SD	0.008	

Note. This table is taken from Sage (1996).

measures of the frequency ranges, the mean frequency (MFREQ), the minimum frequency (MFMIN), and the maximum frequency (MFMAX), which were all positively correlated with each other as a factor. Frequency has been indicated to be one of the most consistent and powerful predictors as to "who" an individual cricket is (Bailey, 1985, 1991; Lloyd, 1981; Thornhill & Alcock, 1983). These results confirmed previous speculations and incorporated the entire frequency envelope as indicative of the isolated male's individual distinctness. The minimum frequency was a particularly strong indicator as to individual distinctness, since it was consistent over all the song bouts (Table 7, $E^2_{rel} = 0.08$). The mean and maximum frequencies continued to appear subject to change since they both were not consistent over the song bouts ($E^2_{rel} = 0.58$; $E^2_{rel} = 0.60$, respectively); however, in the isolated-male condition these were indicative of the calling males. The Isolated-male INTENSITY factor accounted for the intercorrelations between the measures of the intensities within the song parameters, mean intensity (MINT), and mean intensity difference (MINDF) loading negatively with each other as a factor. The INTENSITY factor (dimension) related to the allotment of intensity to frequency components within the syllable. Songs of higher intensity were also characterized by allotting most of that intensity to the mean frequency. In contrast, low intensity songs were characterized by more intensity being allotted to other

frequencies in the syllable. This means that songs produced at higher intensities put that intensity into the mean frequency and had fewer extraneous frequencies being produced in the song syllables. Simply put, if there was a substantial difference between the intensity carried in the mean frequency and the intensity of the syllable as a whole, than other frequencies were present in the syllable. The Isolated-male INTENSITY factor indicated that higher intensity songs had clearer frequency production.

The Isolated-male *STD* factor, since it was composed of the measures of the songs' variances, was involved in the song characteristics' variabilities. Higher factor scores indicated higher variability in the song characteristics; lower factor scores indicated lower variability in the song characteristics. In the Isolated-male condition, the only song variances to interrelate were the differences in the mean intensity and the intensity differences between the crickets. These two song components were positively correlated, such that as the variability in syllable intensities increased so did the variability in intensity differences, i. e., more integral frequencies in the syllable. This result means that songs with more variable syllable intensities also devoted more energy (intensity) to frequencies other than the mean. In the Masters thesis (Sage, 1996), this factor was interpreted as a *CLARITY* factor; assuming that low factor scores would be the

optimum. (low scores imply very little variability, in other words, clarity). The *CLARITY* interpretation suggested that intensity level was maintained at a consistent level, and the syllable intensities were devoted to the mean frequency, i.e. that consistency (low factor scores) in intensity and frequency was important. However, consistencies in the song parameters are not always desirable. Studies of bird song indicate that females habituate to invariant bird song components, leading to a diminishing in female responsiveness. Male birds can overcome habituation in females by varying the characteristics of their songs. Habituation may also be important to crickets. How far away a female is, and how long the female must track the male's calling song, may influence the female's responsiveness. Female crickets may be able to track (to habituate less) variable songs longer and more effectively. At large distances; i.e., when females are distant from males, variability may be an important element in calling song to attract females without habituation. This hypothesis would suggest that variability is more important to isolated males who have to attract females from greater distances. In a situation where females are close by, such as in high population densities, low variability in the song parameters may be more advantageous. Low variability allows for more precise location of a calling male that is nearby. For example, consistent intensity allows a female to track sound

along the intensity gradient: increasing intensity means the male is closer. This hypothesis suggests that males can optimize their attractiveness to females by having low variability in their calling songs in high population densities and avoid female habituation by having high variability in their calling songs in low populations densities. Based on this discussion of variability, this isolated-male *STD* factor was interpreted as a *VARIABILITY* factor.

It is important to note here that none of the temporal song components was represented in a factor. This implied that temporal parameters did not constitute factor variability between isolated crickets, as predicted by Walker (1962), Michelsen (1985), Cade (1979), Popov and Shuvalov (1977), and Thornhill and Alcock (1983). According to Walker (1962) and Michelsen (1985), temporal parameters are affected by temperature and subject to environmental degradation, and as such are not reliable enough to result in sexual selection. Popov and Shuvalov (1977) suggested that temporal features serve as the *essential parameters* for species recognition, and will not vary substantially between members of the same species. Thornhill and Alcock (1983) and Cade (1979) suggested that temporal features lack high energy-consumption and, are, therefore, not fitness related. The three factors specified within the Isolated-male condition are in line with acoustic mate choice theories. All three

factors involve frequency and intensity song parameters; parameters that are unaffected by temperature, calling latency, and are fitness related.

Post-competitive Song Characteristics Factors

An orthogonal factor analysis (using PROC FACTOR TYPE VARIMAX) constructed the following song factors for the post-competitive condition provided in Table 12 (pp. 168). The intermale competitive interactions affected the characteristics of the crickets' songs; the Post-competitive Mean factors were different from the Isolated-male Mean Factors. In the post-competitive condition there was no 'pure' frequency or intensity factor. The frequency envelope found in the Isolated-male FREQUENCY factor was broken apart by separating the minimum frequency from the mean and the maximum frequency. The two intensity components were also separated between the two Post-competitive Mean factors. Post-competitive Mean factor 1 was characterized by the mean frequency, the maximum frequency, and the intensity difference (INTDIFF). The frequency components were positively correlated with each other and negatively correlated with the intensity difference, i.e., the intensity difference decreased when the mean and maximum frequency were at higher frequencies. At lower frequencies, the intensity difference increased, meaning that more extraneous frequencies were present in the syllable. Small sound

Table 12

Post-competitive Calling Song Factors and Factor Loadings

Song Components	Mean Factor 1	Mean Factor 2
Mean Syllable Duration	-0.022	<u>0.708</u>
Mean Intersyllable Duration	-0.010	<u>-0.628</u>
Mean Intensity	0.468	<u>0.515</u>
Mean Frequency	<u>0.850</u>	-0.327
Mean Intensity Difference	<u>-0.567</u>	-0.088
Mean Min. Frequency	0.439	<u>-0.562</u>
Mean Max. Frequency	<u>0.748</u>	0.051
Mean Interchirp Duration	0.002	-0.092
Mean Syllable Number	0.023	0.424
Standard Deviation Factor		
Syllable Duration SD	0.153	
Mean Intersyllable SD	0.372	
Mean Intensity SD	<u>0.896</u>	
Mean Frequency SD	0.168	
Mean Intensity Difference SD	<u>0.916</u>	
Mean Min. Frequency SD	0.072	
Mean Max. Frequency SD	-0.053	
Mean Interchirp Duration SD	0.074	
Mean Syllable Number SD	0.113	

Note. This table is taken from Sage (1996).

producing apparatuses such as the cricket singing assemblies are more consistent at producing higher frequencies (Bailey, 1985). A shift to higher frequencies is easier for the small-bodied cricket, and therefore, higher frequencies are more consistent. This does not, however, explain why these song components composed a factor post-competitively and not also during the isolated-male condition. The crickets have apparently shifted song parameters to produce a different balance of song characteristics due to the competitive interaction. It appeared that the Post-competitive Mean factor 1 remained for the most part a FREQUENCY factor, but it no longer characterized the frequency envelope since the minimum frequency was shifted to Post-competitive Mean factor 2.

Post-competitive Mean factor 2 represented the syllable duration, intersyllable duration, the mean intensity, and the minimum frequency. These parameters related to each other such that as the syllable duration became longer, the intensity became louder and the minimum frequency went lower. The temporal parameters, syllable duration and intersyllable duration, previously lost in the Isolated-male song factors, re-emerged. These two measures constitute what is known as the "duty-cycle," and are normally found linked and negatively correlated (Bennet-Clark, 1989): as the syllable duration increases, it shortens the amount of time available for the intersyllable duration. The minimum frequency and

mean intensity were also part of the Post-competitive mean factor 1. Minimum frequency has a special relationship to body mass, such that the lower the frequency, the larger the male (Bailey, 1991). The minimum frequency is often optimized by adapted or constructed resonance structures in many orthopteran species, implying its tangible role in mate choice. All of the parameters in Post-competitive Mean factor 2 were linked to metabolic energy consumption: longer (more energy in the duty-cycle), louder (more intensity energy), and lower frequency (song effort) songs (Bennet-Clark, 1989). Post-competitive Mean factor 2 was interpreted as an ENERGY factor.

The post-competitive *STD* factor was characterized by the variance in the mean intensities and the intensity differences between the crickets. This Post-competitive *STD* factor had the same song parameter specifications as the Isolated-male *STD* factor and showed only slightly smaller factor loadings, probably due to the fewer number of Post-competitive songs available for the analysis. The Post-competitive *STD* factor was again interpreted as a VARIABILITY factor. The post-competitive condition was characterized by crickets that had just encountered the crowded competitive arena. Environmental effects of the crowded conditions on the behavior of the crickets signify that population conditions were more dense. In dense populations, crickets are clumped together and females are most likely be nearby.

In this situation, it is predicted that low variability in the calling song parameters would be optimal, allowing females more precise locating of the calling males. At high densities, male calling song can additionally function as competitive song interference, to drown out other males (Cade, 1979; Ewing, 1981). Cade's (1979) study showed that males increased their intensities to nearby calling males suggesting that increased and consistent intensities were a behavioral adaptation to high population densities which functioned to drown out song from other males. This Post-competitive VARIABILITY factor may be functioning in one or both of these capacities: localizability or competitive song interference. However, at this point it could not be determined whether or not this VARIABILITY factor was functioning differently between the two experimental conditions. It may simply have been a generalized song characteristic in all crickets or conditions.

Signaling of Phenotypic Attributes in House Cricket Calling Song

The subsequent results for the isolated-male condition were originally presented in an earlier Masters thesis (Sage, 1996), and are expanded here by the addition of standardized regression coefficients for the intercorrelations between the song factors and the male phenotypic attributes. The Post-

competitive condition analyses are entirely original to this dissertation.

General Linear Prediction of Isolated-male Song Factors by Male Phenotypic Attributes

A correlation analysis (using PROC CORR) was performed to test the intercorrelations between the Isolated-male unit-weighted Song Factor scores. The FREQUENCY and INTENSITY song factors were orthogonal to each other ($r = -0.006$, $p = .935$) as created by the orthogonal (VARIMAX) factor methods. The VARIABILITY factor was highly correlated to intensity factor ($r = .769$, $p < .0001$). This intercorrelation was expected since both the INTENSITY and VARIABILITY factor relate to the measures of intensity and intensity difference.

A hierarchical general linear model (PROC GLM) was performed on the Isolated-male condition, using the theoretically-specified male morphological and behavioral attributes as predictors for the three song factors. Theoretical specification and hierarchical testing of the variables reduces the likelihood of alpha-slippage in the model: (1) Theoretical specification reduces the likelihood that irrelevant variables are included in the model, and (2) hierarchical regression procedures use only residualized variance following each variable entered in the model. In hierarchical regression procedures, the variance tested by subsequent variables in the hierarchy is residualized from

the prior variables. The residualized variance continues to be reduced as the modeling procedures hierarchically progress, not allowing subsequent variable to capitalize on common variance. The physical attributes in the isolated-male condition were hierarchically-ordered by entering dryweight (DWGT) first; followed by the between-cricket attributes: body intactness (QUALMEAN), body asymmetry (ASYMMEAN), and color type (COLOMEAN); followed by the idiosyncratic differences of the crickets (CRICKETS); followed by the within-cricket attributes: age (AGE), singing time (TIME), and the number of attempts to record the male singing (ATTEMPTS). The resulting F-values and p-values for the Isolated-male model are shown in Table 13.

Before the intermale competitive interactions had occurred, the isolated-male crickets were signaling body intactness, body asymmetry and body weight in their calling songs. Standardized regression coefficients for these intercorrelations were provided in Table 14.

Table 13

General Linear Prediction for the Male Phenotypic Attributes
Signaled in Isolated-male Calling Song

Physical Characteristics	Frequency		Intensity		Variability	
	F	(p)	F	(p)	F	(p)
DWGT	1.52	(.222)	1.94	(.168)	7.85*	(.007)
QUALMEAN	5.30*	(.024)	0.88	(.772)	0.25	(.620)
ASYMMEAN	0.20	(.656)	13.16*	(.0005)	0.05	(.823)
COLOMEAN	0.45	(.507)	0.13	(.718)	0.07	(.785)
CRICKET	9.10*	(.0001)	1.77*	(.007)	4.21*	(.0001)
AGE	0.18	(.675)	0.02	(.889)	0.02	(.895)
TIME	0.08	(.776)	1.84	(.180)	0.35	(.557)
ATTEMPT	1.33	(.253)	0.07	(.799)	3.10	(.086)
MODEL (R ²)	(0.91)	.0001	(0.68)	.001	(0.95)	.0001

Note. DF F(Cricket) = (76,77); F(Between-cricket) = (1,76);
 F(within-cricket) = (1,77).

Table 14

Standardized Regression Coefficients for the Male Phenotypic Attributes Signaled in Isolated-male Calling Song.

Physical Characteristic	DF	<u>Song Factor</u>
		<u>BETA</u>
		<u>Frequency</u>
Quality	1	-0.11
		<u>Intensity</u>
Asymmetry	1	0.33
		<u>Variability</u>
Size	1	0.18

Note. N = 73

Although not overwhelmingly high, these standardized regression coefficients indicated that isolated-males were signaling phenotypic attributes in their calling song. Male physical quality (i.e. body intactness) was negatively correlated to the frequency of the calling songs. Males with high body intactness sang at lower frequencies than males with less body intactness. As indicated in previous studies (Gwynne, 1982; Simmons, 1988b), lower frequencies were preferred by females. Male asymmetry was positively correlated to the intensity of their songs. Asymmetrical males sang louder songs than symmetrical males. This was an unexpected result. It had been proposed that more symmetrical males would have higher fitness, and therefore,

have higher intensities, as predicted by Thornhill (1995). However, the measure of asymmetry in this study was based on gross anatomical differences, such as broken cerci or antennae, and not on finer morphological measures (e.g., tarsal lengths, file length, the areas of the harp and resonator areas). In addition, this asymmetry measure was obtained at the end of the study; post-competitively and not while the males were in the isolated-male condition. Subsequent bodily damage that was not representative of the isolated male's symmetry may have occurred during the intermale interactions. Male asymmetry was primarily a bodily injury index as was the quality (body intactness) measure. Asymmetrical injuries may have been indicative of a propensity to engage in lifetime aggressive interactions. Finally, male size (dryweight) was positively correlated to the variability of the song intensities and frequencies (VARIABILITY). Larger males produced more variable songs, having a larger range of intensities and additional frequencies in their songs. The large isolated males supplied females with more variable sound sources to track, suggesting a possible habituation function. Male color type, age, attempts, and the time of day were not significantly correlated to any of the Isolated-male song factors. Idiosyncratic cricket variances (CRICKET) continued to account for a significant amount of the differences between crickets' songs; implying that other unmeasured phenotypic

traits may be actively signaled in male calling song that have yet to be specified.

General Linear Prediction of Post-competitive Song Factors by the Social Dominance Outcomes and Male Phenotypic Attributes

A correlation analysis (using PROC CORR) was performed to test intercorrelations between the Post-competitive unit-weighted Song Factor scores. The Post-competitive FREQUENCY factor and ENERGY factor were orthogonal to each other ($r = -0.0521$, $p = .57$) as created by the orthogonal factor methods. The Post-competitive VARIABILITY factor was highly correlated to both mean factors ($r = .638$; $r = .283$, $p < .05$). Again, this was expected, since both mean factors had intensity parameters related to the post-competitive VARIABILITY factor's items.

A hierarchical general linear model (PROC GLM) was performed on the Post-competitive condition using the theoretically-specified social dominance attributes (dominance structures and behavioral factors) as predictors for the three song factors, in addition to the physical attributes. Alpha-slippage was minimized by theoretical specification and hierarchical regression procedures. Furthermore, the number of variables tested in this analysis was superficially large. The conceptual variables (dominance measures) tested were in multiple function forms and not discrete variables; so each different function form of the

conceptual variables was dealing with very small slivers of variance. The dominance structures: despotism (DSD), curvilinear dominance rank (LNMSD), and rectilinear dominance rank (MSD) were hierarchically placed first; followed by the two observed behavioral factors (AGGRESSION and SUBMISSION); which were followed by the between-cricket attributes and their interaction terms (with the social behavioral predictors); followed by the idiosyncratic crickets attributes and the within-cricket attributes. Interaction terms were included in this analysis to examine possible interaction effects between the behavioral and physiological traits. The results for the post-competitive model are provided in Table 15 (pp. 180).

The intermale interactions preceding the post-competitive condition altered the traits the crickets now signaled. Post-competitive songs now signaled the crickets' color type, SUBMISSION behavior items, singing time, body intactness, attempts, and body asymmetry and body mass as interaction effects with the social dominance traits. Standardized regression coefficients for these intercorrelations are provided in Table 16 (pp. 181). The standardized regression coefficients were not overwhelmingly high, but they indicated that post-competitive males were now signaling both social behavioral and phenotypic attributes in their calling song. Male color type and an interaction effect between rectilinear dominance and asymmetry

(MSD*ASYMEAN) were correlated to the Post-competitive FREQUENCY song factor (mean and maximum frequency, and the frequency consistency). Color type was positively correlated to the FREQUENCY factor. Color types were rank-ordered by assigning dark males a value of -1, medium males a value of 0, and light males a value of 1.

Table 15

General Linear Model for the Social Dominance Outcomes and
Male Phenotypic Attributes Signaled in Post-competitive
Calling Song

Physical Characteristics	Frequency		Energy		Variability	
	F	(p)	F	(p)	F	(p)
DESPOTISM	1.98	(.167)	0.95	(.335)	2.89	(.101)
CURVILINEAR RANK	0.16	(.690)	0.10	(.753)	0.86	(.362)
RECTILINEAR RANK	0.01	(.916)	0.13	(.722)	1.29	(.266)
AGGRESSION	0.02	(.896)	2.07	(.159)	0.01	(.927)
SUBMISSION	0.42	(.522)	4.69*	(.036)	0.29	(.592)
DWGT	0.86	(.359)	0.06	(.800)	1.18	(.288)
QUALMEAN	1.19	(.283)	0.09	(.767)	5.88*	(.023)
ASYMMEAN	2.40	(.130)	0.05	(.833)	1.79	(.192)
COLOMEAN	5.31*	(.027)	1.34	(.255)	0.10	(.757)
DSD*DWGT	2.78	(.103)	1.54	(.222)	1.12	(.301)
DSD*QUALMEAN	2.20	(.147)	1.47	(.232)	0.05	(.819)
DSD*ASYMMEAN	2.73	(.107)	0.79	(.380)	0.81	(.375)
DSD*COLOMEAN	0.11	(.740)	0.07	(.788)	0.37	(.549)
LNMSD*DWGT	0.48	(.491)	0.02	(.895)	4.62*	(.041)
LNMSD*QUALMEAN	0.18	(.673)	0.78	(.384)	0.27	(.608)
LNMSD*ASYMMEAN	0.86	(.359)	0.02	(.888)	0.00	(.953)
LNMSD*COLOMEAN	0.02	(.901)	0.01	(.930)	1.25	(.273)
MSD*DWGT	0.00	(.957)	0.01	(.930)	1.02	(.322)
MSD*QUALMEAN	0.39	(.538)	0.00	(.960)	0.62	(.438)
MSD*ASYMMEAN	4.11*	(.049)	0.05	(.823)	0.01	(.913)
MSD*COLOMEAN	0.16	(.691)	0.00	(.997)	2.11	(.159)
AGGR*DWGT	3.24	(.080)	0.11	(.746)	0.16	(.697)
AGGR*QUALMEAN	0.03	(.870)	0.42	(.519)	1.50	(.231)
AGGR*ASYMMEAN	1.34	(.254)	0.33	(.572)	0.49	(.490)
AGGR*COLOMEAN	2.78	(.104)	0.46	(.503)	1.64	(.212)

SUBM*DWGT	1.66	(.206)	0.11	(.743)	0.11	(.739)
SUBM*QUALMEAN	0.29	(.595)	0.18	(.670)	0.07	(.791)
SUBM*ASYMMEAN	0.12	(.735)	1.55	(.221)	0.00	(.971)
SUBM*COLOMEAN	0.00	(.958)	2.28	(.140)	1.45	(.240)
CRICKET	6.67*	(.0001)	6.03*	(.0001)	1.63	(.101)
AGE	1.37	(.248)	0.05	(.832)	1.61	(.215)
TIME	0.17	(.679)	7.72*	(.008)	1.98	(.170)
ATTEMPT	0.78	(.381)	0.74	(.395)	11.01*	(.003)
MODEL (R ²)	(0.92)	.0001	(0.89)	.0001	(0.89)	(.0001)

Note. DF F (Cricket) = (47,46); F (Between-cricket) = (1,47); F(within-cricket) = (1,46). AGGRESSION = AGGR; SUBMISSION = SUBM.

Table 16

Standardized Regression Coefficients for Male Social and Phenotypic Attributes Signaled in Post-competitive Calling Song

Physical Characteristic	DF	<u>Song Factor</u> <u>BETA</u>
		<u>Frequency</u>
Color Type	1	0.15
Linear Dominance*Asymmetry	1	-0.03
		<u>Energy</u>
Submission	1	-0.20
Time	1	0.07
		<u>Variability</u>
Quality	1	-0.03
Curvilinear Dominance*Size	1	-0.08
Attempts	1	0.05

Note. N = 73

This result indicated that lighter males sang at higher frequencies. The interaction effect between rectilinear dominance and asymmetry was negatively correlated to the Post-competitive FREQUENCY factor. Interaction effects were generated by multiplying the two main effects. Interaction effects indicate links between high values in both main effects (Cohen & Cohen, 1983). This interaction meant that high ranking and highly asymmetrical males sang at more intensely produced lower frequencies.

The SUBMISSION behavioral factor was negatively correlated to song energy. More submissive males (males exhibiting more submissive behaviors) sang with less energy than the less submissive males (males exhibiting fewer submissive behaviors). Singing time was positively correlated with energy. More energy was invested in songs sung later in the recording sessions, between the 3 to 5 hours into the L:D cycle. Female peak responsive times were during the 3 to 5 hours after dusk (Cade, 1979), so the males were optimizing their song energy to match these times. Time of day has been associated with vigor of song (Cade, 1979, 1981; Hutchinson et al., 1993). Males that optimize their song output to the times females are most receptive gain a reproductive advantage. There is no advantage in singing high-energy songs during times when females are nonreceptive, e.g., hiding, foraging, resting.

Male quality, attempts, and an interaction effect between curvilinear dominance and size were signaled via the VARIABILITY song factor. Male body intactness (quality) was negatively correlated to variability. High quality males sang with less variability in their intensities and frequency components; in other words, they had clarity in their songs. The interaction effect between body weight (size) and curvilinear dominance rank was also negatively correlated to VARIABILITY; large, high ranking males sang with clarity. Attempts was positively correlated to VARIABILITY. The measure of more attempts needed to record was taken to imply a less motivated male. Less motivated males sang more variable songs. This result for the post-competitive VARIABILITY song factor was different from the isolated-male factor where large males sang with more VARIABILITY. This change was probably the result of environmental changes. Males that have interacted with other males under crowded conditions may infer high population densities through the physical contact. In high population densities, females would probably be closer and could easily distinguish song features. In addition, other males are calling close by. In this condition, drowning out other males may be essential to reproductive success (Ewing, 1981; Forrest & Raspet, 1994). Consistent high intensities may be motivating to females nearby and additionally may function to drown out song by nearby males.

None of the main dominance effects was indicated in male calling song, only within interaction effects. Within these interaction effects, rectilinear and curvilinear dominance affected signaling characteristics. Despotism was put to rest once and for all as a hypothetical structural effect on either aggressive behavior and singing behavior. This implied that only high ranking males continued to signal fitness related qualities of asymmetry (here interpreted as injury due to motivation to engage in aggression) and size. Dominant males sang with more energy as implied by the submission factor indicating low energy songs. These results implied that female choice advertisement in the males' calling song was affected by the intermale interactions, such that a cricket's dominance status affected the traits signaled in calling song.

Male age was not related to any of the song factors. In both models, cricket idiosyncrasies continued to account for a significant portion of the variance. It could be these variances that signal the physical traits not correlated to any on this study's song factors. Several potential song structure parameters were not examined in this study, that may still be active in female choice.

DISCUSSION

The methodology of this study was marked by its use of Probabilistic Functionalism as a representative design (Petrinovich, 1979), which requires inclusivity, external validity, and generalizability. These requirements were accomplished by testing all relevant variables, sampling across situations, and maintaining the ecological context of the behavioral circumstances. This representative design modeled the complexity of male signaling of mate quality stimuli available to females for making mating decisions. The inclusive and naturalistic framework allowed for the evaluation of the multiple, interactive, and dynamic properties of male mate quality signaling.

The large number of physical and behavioral male traits and their causal networks that result in the production of calling song were evaluated. This study started at the source of male song, the male cricket. It acknowledged that each individual male was a whole package of phenotypic traits, all interacting together and influencing the song that the males produced. No one trait was evaluated in the absence of all the others. To evaluate the direct and indirect effects these traits had on the production of male calling song, multiple phenotypic traits and multiple song parameters were evaluated.

The principal outcomes of this study were that: (1) Male calling song characteristics, in a laboratory population of house crickets *A. domesticus*, signaled information about the males' phenotypic attributes. More specifically, males signaled information concerning fitness related attributes associated with female choice. (2) The male crickets established linear dominance hierarchies when they were allowed to interact. The dominance rank a male achieved within these hierarchies determined whether the male continued to sing and what was signaled in his calling song. And finally, (3) the male crickets altered their calling song characteristics following the intermale competition to signal dominance status (Figure 5, pp. 202).

Signaling of Female Choice Parameters in Isolated-male Calling Song.

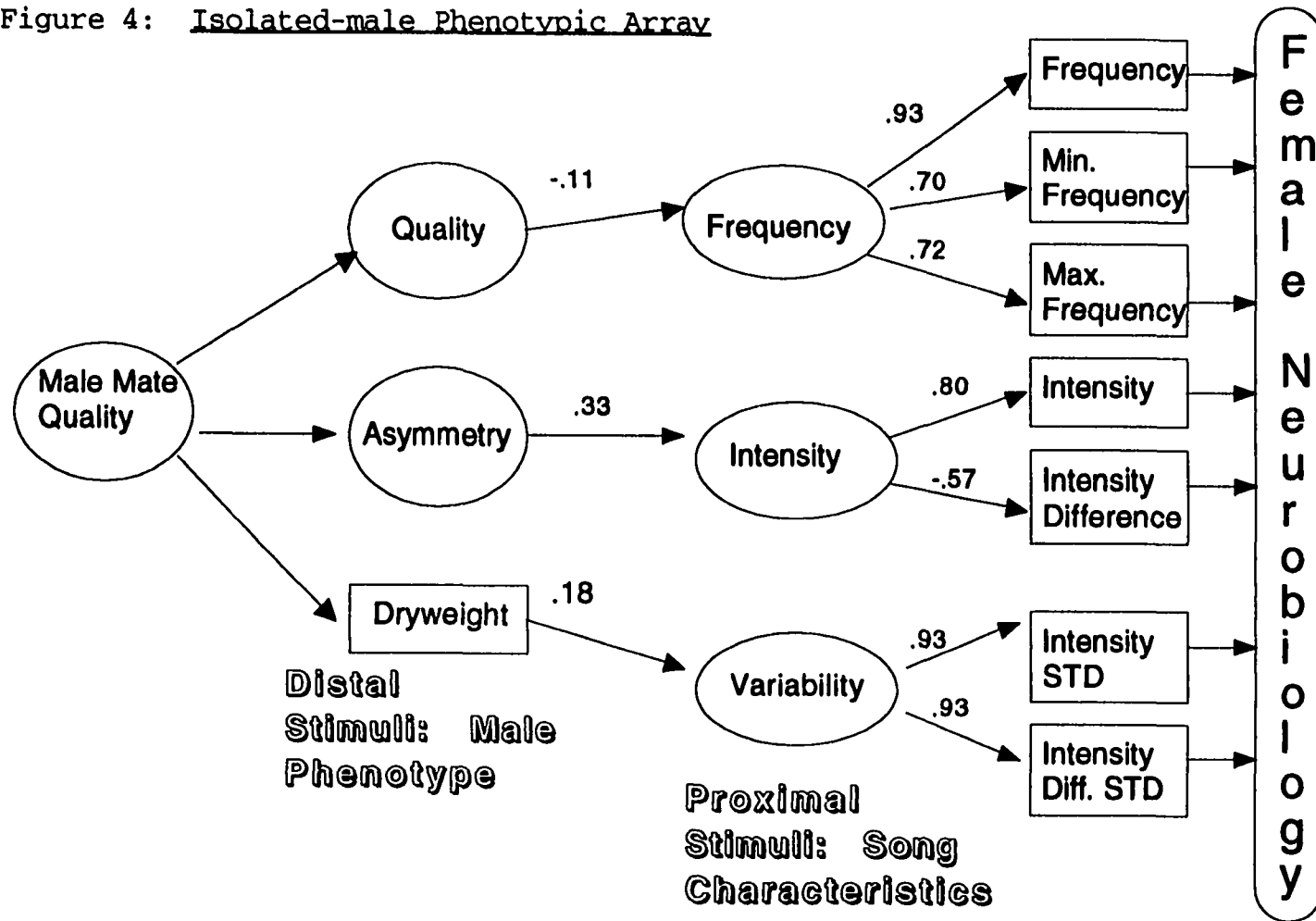
Isolated males signaled information in their calling songs concerning fitness related phenotypic attributes associated with female choice. These phenotypic attributes were male size (body mass), body asymmetry, and quality (body intactness) (Table 13, 14). These distal phenotypic attributes were signaled via proximal stimuli in three song factors (Table 11): FREQUENCY, INTENSITY, and VARIABILITY. These three factors were composed of the intensity and frequency components of the males' calling songs, as

predicted by Thornhill & Alcock (1983). The full causal relationships of the phenotypic array for the isolated-male condition are provided within the conceptual framework of the lens model in Figure 4.

FREQUENCY, composed of the frequency envelope, was negatively correlated to male quality (body intactness). Males with high body intactness sang at lower frequencies than less intact males. These lower frequencies encompassed the full ranges of frequencies within the males' chirps. This result was consistent with Thornhill and Alcock's (1983) prediction that song frequency would be a probable cue to male fitness. High male quality indicated the male's ability to avoid developmental difficulties, pathogens, and parasites; and to survive the severity of intermale competition (Bailey, 1991). Studies have indicated a female preference for lower carrier frequencies, in *T. cantans* (Latimer & Sippel, 1987), and in bushcrickets *R. verticalis* (Schatral, 1990).

INTENSITY, composed of the mean intensity and intensity difference, was positively correlated to male asymmetry. The results indicated that more asymmetrical males sang with higher overall intensity. This finding was contrary to the hypothesis that more symmetrical males would be found signaling with greater intensity. The regression coefficients revealed a positive correlation between increasing asymmetry and louder songs. It was apparent that

Figure 4: Isolated-male Phenotypic Array



the asymmetry measure of this study was measuring something other than developmental asymmetries as specified by theories regarding symmetry (Møller, 1993a; Parsons, 1990; Simmons, 1995; Thornhill, 1993). The asymmetry measure in this study was actually a measure of unbalanced accrued bodily injuries and possibly a "motivation to engage in injurious behavior." This last characterization of this asymmetry variable is probably more accurate, since males were signaling it in their calling song. In addition, these asymmetry measures were not taken at the time the isolated-male songs were sung, but after the competitive interactions. A more accurate correspondence between song intensity and male symmetry might have resulted from more longitudinal measures of symmetry or to finer discriminations of the males' morphologies.

VARIABILITY, composed of the standard deviations in the intensity and intensity difference, was positively correlated to male size (dryweight). Size was signaled by the variabilities in the song intensities and frequencies. Females of many insect species prefer larger males (Thornhill & Alcock, 1983), as has been found in field crickets (Simmons, 1988, 1992; Simmons & Zuk, 1992). Halliday (1983) and Zuk (1989) have suggested that size is an indicator of health, nutrition, and parasite resistance. Larger males demonstrate the ability to acquire food and avoid parasites. Larger males win more fights during intermale competitions (Bailey, 1991; Thornhill & Alcock, 1983). In addition, a

larger size allows males to sing at lower frequencies and sing louder because the singing assemblies are larger (Bailey, 1991). This song factor was unique in that it was characterized by variability, something not found in crickets before. Large males were singing a greater range of intensities, not one steady loud intensity as implied by many other studies (in bush crickets, Bailey & Yoeh, 1988; in mole crickets, Forrest, 1983; Forrest & Green, 1991; Simmons, 1988a). In addition, the larger males were singing with more intensity in their syllables being devoted to noncarrier frequencies. This finding was unique and original for a study in cricket bioacoustics, however, in bird studies this finding is rather common. Male birds will alter their song characteristics to prevent habituation in females. Could this be happening in crickets? A follow-up study on the female response array should take habituation in female crickets into account.

The standardized regression coefficients describing the relationship between the male phenotypic factors and the song factors served as the ecological validities for these song cues. These coefficients were generally small overall, indicating that the genotypic and phenotypic variabilities between the males were small. This finding can be explained in terms of rearing conditions and experimental design. (1) All the crickets were bred in a captive population, where crowded conditions heighten the effects of sexual selection

and inbreeding. (2) All the crickets were singers in order to be incorporated into the experiment. This eliminated lower quality nonsinger males from being evaluated.

Social Dominance in House Crickets

The environmental effect of placing the males into a small, crowded arena not only caused competition and dominance outcomes, but probably, also, altered the crickets' behavioral responses due to population density changes. The production of the isolated-male song features suggested that under circumstances of low population density the optimal strategy of the male crickets was to generally broadcast female choice parameters. When population densities are low, females are scarce and scattered at large distances which makes calling more optimal (Alexander, 1961, 1975; Bailey, 1991; Cade, 1979; Hissman, 1990). In addition, there are no other rival males who might actively attack the calling male in response to what is being signaled. At higher population densities, males and females are encountered more frequently and alternative strategies, such as satellite behavior, or searching for females, have increasing benefits (Alexander, 1961; Cade, 1979). In addition, calling in high population densities increases competitive encounters which require the competitive power to back up the song, and thereby, increases the costs to calling. Some theories of female choice suggest

that females cause intermale competition by choosing males based on the outcome of male competition, thereby weeding out the weak or sickly before mating decisions are made (West-Eberhard, 1984). Dominance contests insure that high ranking males have been tested for the authenticity of their physical prowess and aggressive motivation.

There were several matters involving the dominance constructs which had to be verified before dominance rank could be used as part of the male phenotypic array. (1) It had to be determined whether cricket behaviors could reliably be observed, and were reliably consistent and systematic (fell into predictable patterns of behavior). (2) It had to be determined whether the behavioral patterns exhibited by the crickets could be characterized by the generalized construct of dominance relationships. Finally, (3) the dominance relationships had to be characterized in terms of hierarchical structures in order to assign meaningful ranks to the individual crickets. A meaningful rank was one that reasonably characterized a cricket's behavioral participation and outcome in the intermale competitions. Once these social dominance issues were resolved, the crickets could then be assigned dominance ranks as part of their overall phenotypic profile.

Hierarchical Relations Among the Male Crickets

The introduction of originally isolated males into the highly populated arena dramatically affected the behavioral patterns of the males. Immediately after being introduced into the competitive arena, intense fighting and aggressive singing ensued between the males. Asymmetrical patterns of agonistic behaviors defined as aggression and submission resulted. The patterns of sixteen notably aggressive and submissive behaviors (Table 1, pp. 110) were amply characterized by evoking the concept of dominance ($r = .74$), particularly the aggressive behaviors. Distinguishable dominance hierarchies were established within a few hours as indicated by the temporal stabilities of the subjective dominance ranks within the formation period of the observations.

The concept of dominance order was a useful index as to the patterns of aggression among the males (Table 4) ($R^2 = .61$). To a lesser extent, the dominance orders also explained the patterns of submission ($R^2 = .25$). The implications of these findings were that the submissive behaviors were possibly functioning in alternative behavioral domains, other than as a response to aggression. A look back at Table 1 (pp. 110) which operationally defines the behavioral items reflects that submission is more a passive response to the action of aggression, and is defined in terms

of another cricket's action upon the focal cricket. Submission involves the lack of an active aggressive response to another's aggression. For example, in the interactions between the males, the behavior *is threatened* was usually followed or returned by *threatens*; a mutual behavioral sequence. However, as the social interactions progressed, many subordinates failed to complete the behavioral sequence, instead they merely remained unresponsive or withdrew. Subordinates could not be incited to aggress, whereas the higher ranking individuals continued to aggress at the slightest provocation (e.g., seeing or hearing other crickets in their vicinity).

Three structures of dominance order were considered and tested as possible hierarchical outcomes of the competitive interactions: despotism, curvilinear order, and rectilinear order. *A. domesticus* are mostly gregarious and not territorial, for this reason, territoriality was not considered a likely competitive outcome. In field crickets, a substantial amount of agonistic behavior revolves around the possession of a calling territory, because territorial ownership results in higher male mating success (Alexander, 1961; Burk, 1979; Cade, 1979). These conditions hold true for territorial species, and such is the case for numerous vertebrates and invertebrates. House crickets, however, live in groups and form group lekking areas, and would not follow territorial patterns. For more social species, a despotic

social structure would correspond to territoriality; the despot, however, tolerates subordinates in his territory more readily than a territorial resident. Like territoriality where males fight for possession of the area, in a despotic condition males fight for the top position. Despotism, however, implies patterns of behavior characteristic of subordination, an alternate strategy for survival and probably for limited mating success among the defeated males. As Alexander (1961) and Cade (1979) suggest, in high population densities, satellite behavior is more beneficial due to random encounters with females and a saturation of males. As population density declines, territorial possession and calling behavior becomes more beneficial. Despotism is distinctive because subordinates continue to occupy the same area as the despot, this requires behavioral control by the despot since subordinates may interfere with the despot's access to females. In addition, despotism requires the evolution of submissive behavioral responses and behavior patterns. Alexander (1961) and others have noted that typical territorial field crickets often fight to the death (as attested by its popularity as a sport in the Far East), implying limited submissive behavioral responses. Any species attaining social living groups must have submissive behavioral responses and accepted subordinate positions within the group, and this entails dominance relationships.

The degree of social dominance organization can be theoretically specified and tested for individual species. As a species moves away from strict territoriality (due mostly likely to limited area and forced proximity), despotism would be the most logical subsequent dominance structure to evolve. Despotism approximates the closest structure to territoriality in a social species. There are several specific characteristics of despotism. (1) There are only two meaningful rank positions, despot and subordinate, which should be characterizable by the differential behavior patterns between the despot and the subordinates. (2) The despot controls the access to all resources. (3) The behavioral differences between the subordinates do not represent dominance relationships, all subordinate hold the same position.

Once dominance relationships arise between the subordinates, i.e., differential patterns of agonistic behavior, then the dominance structure is no longer despotic, and a more linear relationship among the individuals must be specified. There are several conditions that could potentially promote dominance relationships among the subordinates, specifically if different levels of status provided different levels of access to resources. If being the second ranking individual in a hierarchy allowed for increased survivability and mating success, then contesting over that position would be beneficial. The same can be said

for the third and fourth positions, as long as a fitness advantage is achieved by simply being a rank higher, e.g., third instead of fourth. If each rank within the group was equally better than the rank below it, then a rectilinear dominance structure would ensue. A curvilinear dominance structure would arise if the benefit-to-cost of achieving a rank steadily declined with decreasing rank; the second ranking position may be advantageous, but the benefits of the third position may simply not be worth contesting over. In more highly dense populations, females are more readily available, so differential access may be more beneficial. A linear dominance hierarchy implies that the top position (rank 1) is not the only contested position, as despotism implies. Linear dominance hierarchies imply differential "rights" of access. The various attained levels within the group have differential mating success. If the dominant male is occupied with a female (or other activities), then second ranking male has priority access to any newly available female.

Despotism was rejected as a potential dominance structure by the analyses of this study indicating that the social structures among *A. domesticus* males were more hierarchical. The results of this study indicated that dominance structures in *A. domesticus* were linear hierarchies; ranks within the social structure were meaningful. Dominance hierarchies in *A. domesticus* males

have been observed in other studies which assumed the dominance structures were linear, but with no actual tests of the structures were made (Crankshaw, 1979; Phillips & Konishi, 1973). Analyses of the three dominance structures (see Figure 1; pp. 65) resulted in different function forms explaining the patterns of the agonistic behaviors. More specifically, the results indicated that submissive behaviors were curvilinearly related to dominance, and the aggressive behaviors were rectilinearly related to dominance. Rates of the submissive behaviors logarithmically increased for lower ranking individuals. The curvilinear nature of the submissive behaviors indicated that higher ranking crickets were infrequently approached or engaged by other crickets in agonistic interactions. Lower ranking crickets were frequently engaged, but did not respond with the appropriate agonistic behaviors, in other words, subordinates acted passively to aggressive engagements. The rates of aggressive behaviors resulted in a rectilinear dominance order; aggressive behaviors uniformly decreasing with decreasing rank. Most studies of dominance in crickets have focused on aggressive behavioral outcomes, this study which included submissive behaviors noted a pattern of curvilinearity in submissive behaviors.

The social complexity of behaviorally obtained rectilinear dominance order among crickets is surprising, since it is behaviorally established, unlike the "social

insects" where social placement is based on rearing environment and hormonal control (bees, ants, termites: Wilson, 1975). The environment of *A. domesticus* appears to have selected for well organized behavioral dominance orders. It remains to be determined whether the various rank status' are meaningful to the females and affect their mating decisions. In social primates, the various male ranks are linked to differential mating success (Bernstein, 1981). A follow-up study pursuing male mating success based on rank status's in crickets would be enlightening.

Behavioral Changes to Singing and Singing Activity due to Dominance Rank

The most obvious effect of the competitive interactions was on the singing activity of the lower ranking males. Lower ranking males were more likely to die and less likely to sing calling song after the dominance encounters. The deaths of lower ranking males may have resulted from two causes: (1) the severity of the dominance encounters and (2) possible prior weakness or lack of health in the male resulting in both low rank and death. In addition to dying more often, lower ranking males decreased their singing activity. The primary reason for this finding was clearly apparent to the observers of the videotaped competitive interactions: singing by lower ranking males elicited attacks by the dominant males, seen in other studies as well

(Cade, 1979; Dadour & Bailey, 1985). This overt control of singing behavior has been found in several bird species. In brown-headed cowbirds, dominants sing a potent song, nondominants singing potent song are attacked.

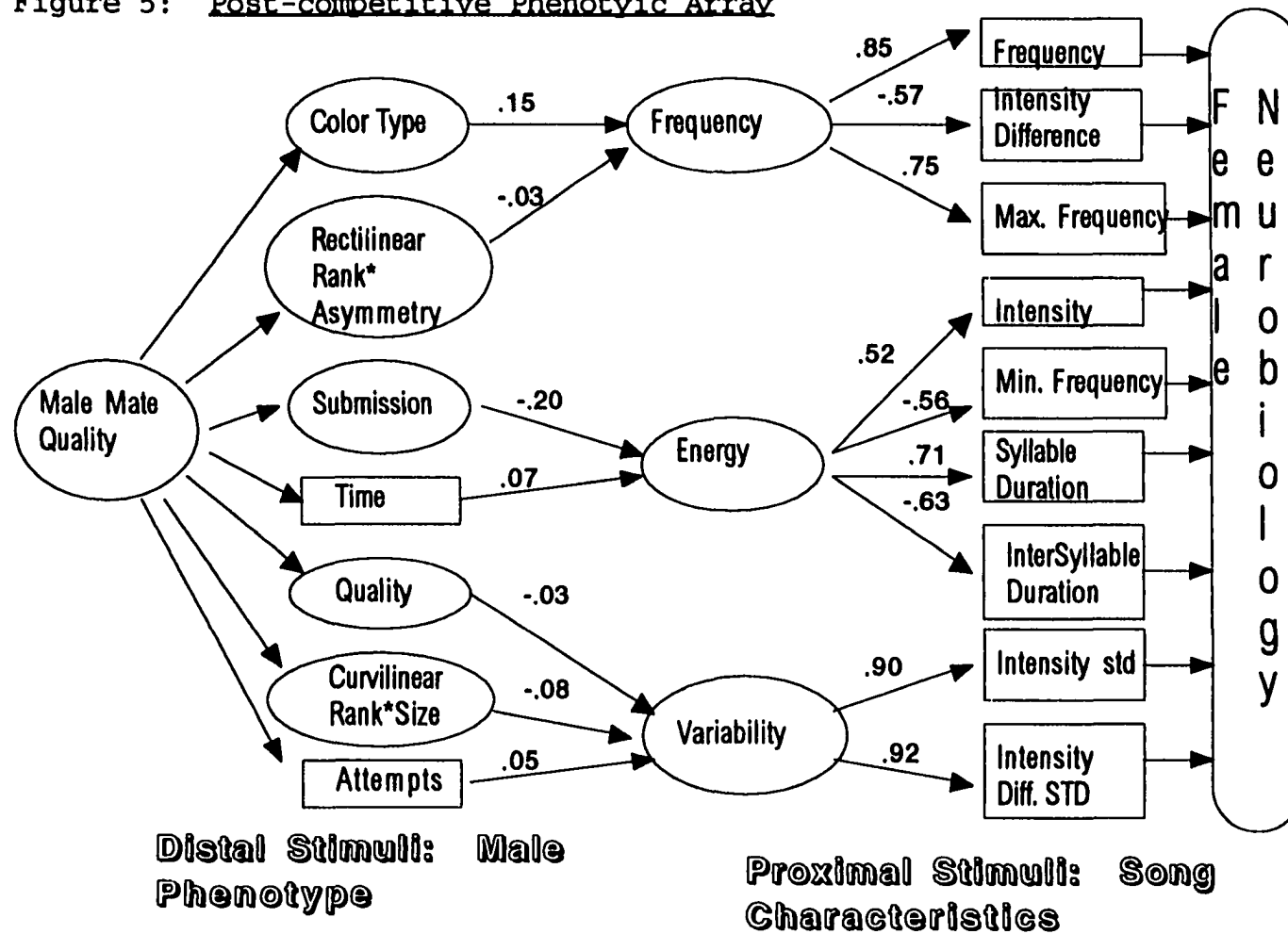
Cade (1979) found similar results in his study of *G. integer*, and suggested that lower ranking males were adopting alternative strategies. Thus, a second reason for fewer post-competitive songs from the lower ranking males may be due to behavioral shifts to alternative strategies such as satellite behavior. In the behavioral observations of the dominance groups, several different alternative behaviors to singing were observed: (1) optimal spacing patterns among the males with only the dominant male calling, (2) satellite behavior, one silent cricket remaining near the calling dominant, (3) dispersal behaviors, attempts to leave the competitive arena, and (4) pseudofemale behavior, one male courting another. This pseudofemale behavior was characterized by an approaching male which acted passively to the other male, a female's sexually responsive behavior (Alexander, 1961). This suggested the possibility of pseudofemale behavior as an alternative male strategy in crickets. Further evaluation of the dominance videotapes may reveal complexities in these alternative behaviors not specifically looked at in this study.

Signaling of Social Dominance in Post-competitive Calling
Song

The intermale competitions and the resulting dominance outcomes had a profound effect on the male calling song characteristics. The calling song characteristics were specifically altered to signal dominance status. The changes to calling song following the intermale competitions suggested that the signaling of female choice parameters was being obscured or enhanced by the outcome of dominance encounters. The intermale competition was specifically targeted at suppressing lower ranking males from singing and from signaling mate quality, thereby denying access to the means to attract females. High-ranking males continued to enhance their mating success by signaling their dominance status, and continuing to signal fitness related qualities. This outcome suggests that intermale competition may actively interfere with the "ideal" signaling of mate quality in lower ranking males.

Following the intermale interactions, higher ranking males continued to sing high intensity, low frequency songs with very little variability in their intensities and frequencies (Figure 5). These song characteristics signaled the male's rank and quality.

Figure 5: Post-competitive Phenotypic Array



After the competitive interactions, many lower ranking males ceased to sing. Lower ranking males that continued to sing, ceased to signal features of mate quality. Lower ranking males sang softer songs at higher frequencies and with greater variability.

The dominant males were able to force modification of the calling songs in lower ranking proximate males, thereby potentially changing the outcome of female choice, by changing the constitution of the choice medium. Bird song studies have found similar outcomes. In the brown-headed cowbird, the dominant song can only be sung by the dominant male (Dufty, 1986). Subordinate males sing subordinate songs. A subordinate cowbird attempting to sing the dominance song is attacked by the dominant bird. These results are congruent with the observed videotaped dominance interactions in the crickets, which revealed suppression of singing in other males by physical attacks from the dominant male. Follow-up ethogram data obtained from the dominance interaction videotapes will undoubtedly confirm these subjective observations.

This study identified several song parameters in the stimulus array that were affected by the intermale interactions (Figure 5). The mere fact that the males' calling songs changed by the apparently simple introduction of intermale competition supported the notion that dominance position was being signaled. Following the intermale

competition, alterations in the song features resulted in three song factors: FREQUENCY, ENERGY, and VARIABILITY. The minimum and maximum frequencies separated on to different song factors. The intensity components separated on to different song factors. And, temporal song structure changes occurred after the competitive interactions. In the isolated-male songs, none of the temporal song parameters were important. In the post-competitive songs the syllable and intersyllable durations reemerged; specifically the syllable durations were lengthened and the intersyllable durations were shortened by high ranking males (larger duty-cycles). Active temporal altering of calling song has been noted in studies of chorusing in field crickets (Bailey, 1991), and in response to increases in the male population density (Ciceran et al., 1994). Apparently, aspects of temporal structure can be freely altered by males in response to intermale interactions; males also alter their song characteristics when they sing rivalry song or courtship song.

The post-competitive FREQUENCY factor now characterized the mean and maximum frequencies, and acquired the intensity difference parameter. Lower frequencies were indicative of higher ranking and asymmetrical males. A factor emerged post-competitively that was characterized by the duty-cycle, the minimum frequency and the mean intensity. This factor was interpreted as an ENERGY factor, because all of these

song components are involved in overall energy output. High ranking males sang with more energy. The final post-competitive factor was VARIABILITY, which was negatively correlated to quality, size, and dominance. Large, high quality, high ranking males sang clearer, more consistent songs, in terms of intensity and frequency differences.

The ENERGY factor was a particular enigma. All three of the factors song parameters, mean intensity, minimum frequency, and lengthened syllable duration were associated with energy consumption. Effort must be expended to sing longer, louder, and at lower frequencies. These three components together, constitute a "prototypical" factor of energy output. Why this factor emerged post-competitively and not during the isolated condition is baffling. It is assumed that higher fitness males would uniformly optimize their energetics, in spite of dominance status. It is not clear why this factor emerged due specifically to the dominance interactions, other than lower ranking males were singing with less energy; a constraint probably inflicted on them by the higher ranking males. Quieter songs allowed the lower ranking males to continue singing but without being attacked by higher ranking males, as noted by Cade (1979). The ENERGY factor was also associated with time of day. The males were optimizing their energy output to correspond with female receptive periods. Again, it is interesting that males were optimizing singing times only post-competitively.

It can only be speculated that this result corresponded to competition for the optimal singing times, where the higher ranking males were monopolizing the best singing times.

The post-competitive VARIABILITY factor was a change from the isolated-male VARIABILITY factor, although the same song parameters characterized the factor. In the isolated condition, large males sang highly variable songs. Post-competitively, large high-ranking males sang invariable songs. The change in significance of this song factor is probably directly related to the crowded competition arena. The males were crowded into close proximity with three other males. This probably triggered response behaviors to the high population density conditions. Presumably, in dense populations, females are closer by and can easily distinguish song features. In addition, other rival males are close by calling. Consistent high intensities may serve to drown out surrounding males, provide more precise song cues for nearby females to locate, and may be more motivating to the females.

In simple terms, the crickets actively changed the dynamics of their singing in response to competitive intermale interactions. These results implied that mate quality signaling in the male's calling songs were affected by the intermale interactions, such that a male's dominance status affected the traits he could signal. These findings suggest that in species whose males contribute nothing but sperm, intermale competition may have been selected for its

role in suppressing and obscuring male mate quality signaling by the suppression of singing and song characteristics in rival males. The behaviors of intermale competition were a mechanism to manipulate the outcome of female mate choice by controlling access to singing, to singing potent songs, and to optimal calling times. The answer as to how dominance is signaled via calling song is through the following features: high consistency, low frequency, high intensity, and larger duty-cycles.

Individual Differences in Song Characteristics and Male Phenotypic Attributes

An intervening problem that had to be resolved during this study was whether or not individual calling songs had systematic individual differences between males; and which specific song parameters were distinctive (separating the species-typical parameters from the individual "signatures"). As expected, some song components were not idiosyncratic for the individual crickets. These components were the chirp rate, chirp and interchirp duration, (as predicted by Alexander, 1961), and syllable number. Chirp duration and interchirp duration were too highly variable within individual crickets to indicate systematic phenotypic differences. The syllable number was invariant between the males and was obviously a species-typical song

characteristic. All of the other remaining song components demonstrated systematic idiosyncratic differences between the males and their calling bouts. Song components that varied between individual crickets were syllable duration, syllable intensity, mean frequency and minimum frequency. Song components that varied between individual calling bouts within the crickets were mean frequency intensity, intersyllable duration, and maximum frequency. All of these song characteristics involved frequency and intensity components, with the exception of the syllable rate. However, including syllable rate, all of these features involve energy output; song parameters which cannot be faked by possible cheater males since only healthy, large, and, dominant males can expend the energy (Hutchinson et al., 1993).

It is important to note here that all crickets in this study were selected on the basis of their song capabilities (i.e., each cricket had two song recorded while isolated). This means that the crickets in this study were all healthy enough to expend large amounts of energy on singing; weaker males did not meet the study's requirements. This selection accounts for the large numbers of crickets that were purchased but did not make it into the study. In fact, subsequent descriptive statistics not reported in this dissertation indicated very little variation among the morphological attributes (size, quality, asymmetry) of the

males in this study. It is interesting that the song characteristics differences were so definitive as to the signaling of even these fine morphological differences among the males.

The factor analysis revealed quite obviously that the song factors from the isolated-male songs were different from the post-competitive song factors. These song characteristics alterations were apparently in response to the intermale interactions, suggesting that the calling features either (1) had acquired a competitive function, (2) were now signaling dominance status, or (3) both. This result agreed with the hypothesis that song features would change due to interactions with other males and was consistent with Phillips and Konishi (1973)'s assertion that calling song in *A. domesticus* serves to warn other males. These song alterations were also consistent with a shift in behavior patterns in response to increased population density (Alexander, 1961; Cade, 1979; Ciceran et al., 1994; Dadour & Bailey, 1985; Hissman, 1990). Subsequent analysis with the male phenotypic profiles, including dominance ranks, showed that males altered their songs in accordance with their dominance status. The signaling of dominance alone could serve both a competitive and sexually attractive function, since the response to calling song depends on the respondents. Females may be attracted to the dominance signal, as found by Crankshaw (1979), and males may be

intimidated or incited to aggress to the dominance signal, as found by Dadour and Bailey (1985). Therefore, the outcome of intermale competition may be influential in the females' mating decisions. As suggested by Searcy and Andersson (1986), female choice parameters may be impossible to differentiate from those determined by intermale competition.

One interesting finding in this study was the lack of temporal song parameters in the song consistencies and the song factors. Although syllable duration and intersyllable duration were retained for factor analysis, these were not part of the isolated-male song factors. This finding accords with many other studies that have found that temporal changes are due to temperature (Walker, 1962), population density, and time of day (Ciceran et al., 1994), but not fitness related traits. Simmons (1988), however, found in *G. bimaculatus* (De Geer) a correspondence between the syllable rate and the chirp rate due to male size. These temporal features, syllable and chirp rates, were not found to be related to physical characteristics in this study. The syllable rate, however, was affected by intermale competitions, such that subordinate males sang with shorter syllable rates. There are several explanations for this lack of temporal song parameters in the calling song characteristics.

(1) Temporal components may be the *essential recognition* features that communicate species identity, as suggested by

Popov and Shuvalov (1977). All males of a species evolve to sing the species-specific song characteristics. The energy costs invested in the temporal features are minimal to those invested in intensity and frequency (Thornhill, 1993). All the males in this study were singers and were generally of high quality. Ineffectual singers may gain so little and incur such great costs that singing a "wimpy" song is worse than not singing. The *motivational features* of calling song are probably those that come with energy and competitive cost. This study supported this notion.

(2) Temporal song features are substantially affected by environmental factors: temperature (Ciceran et al., 1994; Walker, 1962), rearing environment (Olvido & Mousseau, 1995), distance (Simmons, 1988), and vegetation/ground composition (Michelson, 1985). One of the most consistent findings is that temperature affects temporal components (Ciceran et al., 1994; Doherty & Callos, 1991; Simmons, 1988, 1995; Walker, 1962). Walker's (1962) early experiments demonstrated that female crickets' nervous systems were coupled with the temperature effects on calling song, such that females optimally track song factors produced in the same temperature corresponding to the temperature of their nervous systems. If females ignore temporal patterns of differing temperature, then males that vary their temporal factors outside of the temperature effects will lose matings with the temperature-

coupled females. Temporal song factors may not be reliable cues to utilize as female choice parameters.

(3) Another explanation for lack of temporal song features is that repeated song stimuli lead to female habituation to those stimuli, as suggested by West-Eberhard (1984). The evidence of this occurring in birds is well substantiated. Males may vary their temporal patterns in order to reduce female habituation to their song. It was speculated that variability in cricket song temporal patterns may be an evolutionary response to habituation in the female cricket. The VARIABILITY song factor found in the isolated-male condition served to substantiate this notion. Female habituation is poorly understood; few studies have attempted to determine its effects in female crickets.

Morphological and Behavioral Differences Between Crickets

All the males in this study were of relatively high quality, however, the intermale competitions were intense enough to promote subordination and alternative behavioral strategies. As stated above, asymmetry was more of a measure of "motivation to engage in injurious activities", since true developmental measures were not taken. For this study, it appeared that the asymmetrical males were more motivated to sing and aggressively engage in the dominance struggles. The asymmetrical males of this study were the healthier, more motivated singers. One reason why finer, more developmental

morphological measures (such as harp areas, tibial and femoral lengths, file lengths) were not taken was that the procedures necessary to make these measures were invasive and could inflict harm to the crickets while they were still in the study. A possible confound to this study was that the life history measures of asymmetry and quality were not assessed (i.e. these measures were not taken for each song recording), since all morphological measures were obtained after euthanization at the end of the study. Injury over time may have accrued limiting the magnitude of these singular absolute measures.

Future Directions

Substantial interindividual cricket differences, unexplained by the phenotypic traits measured, accounted for significant amounts of the variation in the male calling song. It is likely that other possible male phenotypic attributes and environmental sources of variance may explain these song characteristics. The potential signaling capacities of cricket calling song are far from exhausted. The answer to these other song variabilities probably lies in finer morphological discriminations of the song assemblages, e.g., the tooth number, file length and the area of the harp and resonance areas.

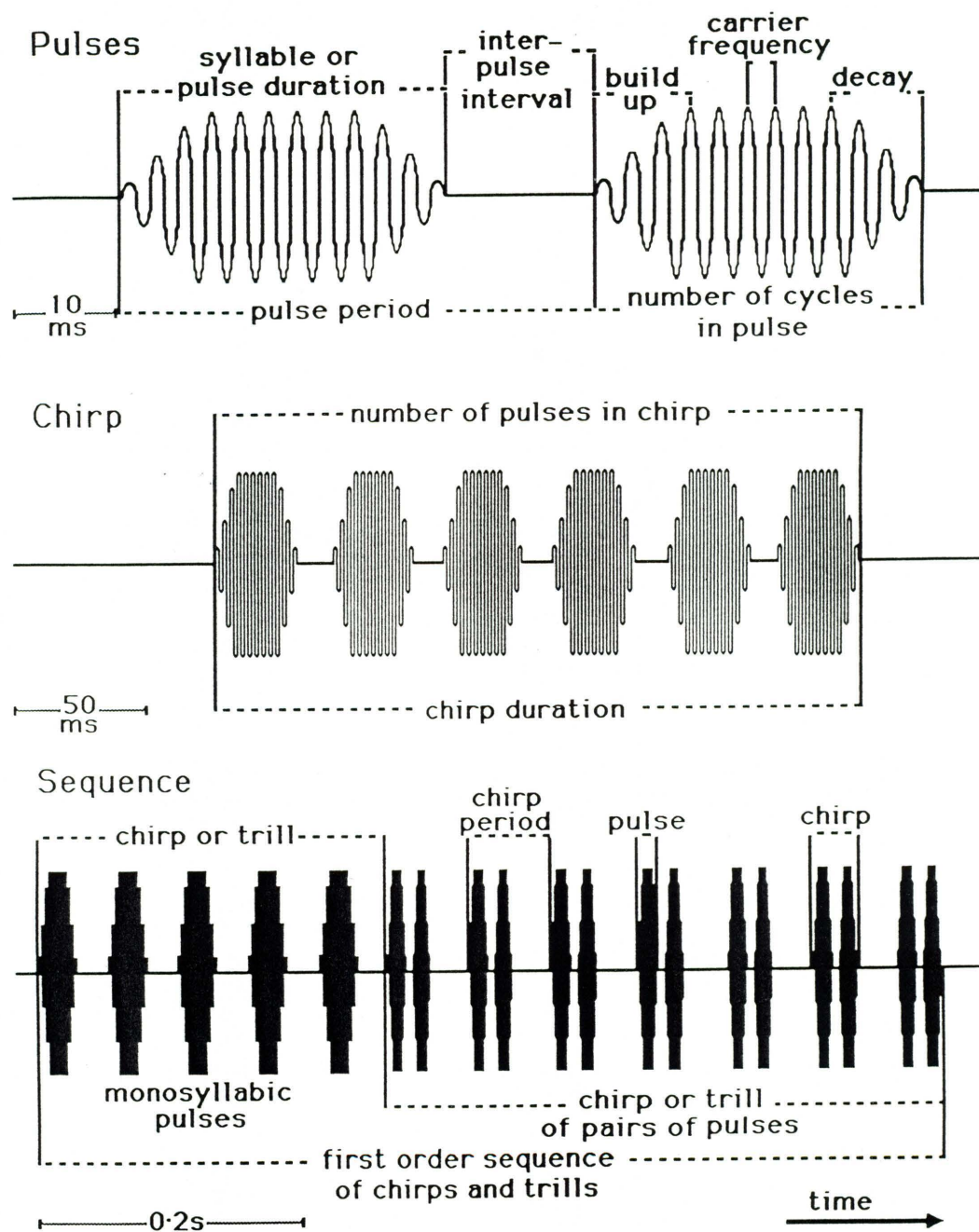
The ramifications of this study, that males signal their phenotypic profile via their calling song, suggest that

females do attend to these cues and use them to make mating decisions. The obvious future direction of this study is to determine the females' responses to the song cues, and measure the functional utilities of those responses. There are several avenues into which the female mating decisions can be explored. One obvious question continually brought up throughout this discussion is whether the females attend to these cues. Specifically, do females make mating decisions based on the phenotypic information in the calling songs? Second, do the females attend to the dominance signals in the post-competitive songs? Several experimental conditions may be contrived. If population density is an important factor to the calling song characteristics than isolated females and densely populated females may response differently to the songs from the different conditions. This study also suggests research into the meaningfulness of the males' ranks to the females. Will the females be able to determine the rank of the males based on their songs? In addition, the issue revolving around female habituation to cricket calling song remains to be answered.

Finally, Ewing (1989) suggests that males are respondents to calling song as well. In addition to examining the female responses, male responses could also substantiate issues involving the signaling of phenotypic information in calling song. Will males respond differently to the songs of differing ranked males? For example, will

subordinate males avoid the calling speaker and will dominant males attack it. In addition, the existence of covariation between genetic quality and environmental constraints remains an issue for further research.

APPENDIX A

Characteristics of Cricket Calling Song

From Bennet-Clark (1983), pp. 229. Used with permission.

APPENDIX B

Cricket Ethogram Behavior List

Marks	FA drags anus on substrate.
Autopreens	FA grooms self.
Solitary, rest	FA rests alone with body laying on surface and antenna held parallel with body.
Solitary, alert upright.	FA stands alone with body held off the surface and antennae held
Eats	FA eats edible.
Drinks	FA drinks.
Locomotion	FA walks, climbs, or jumps more than one bodylength.
Digs	FA digs in substrate with legs.
Investigates, environment	FA probes environment with antennae.
Investigates, other	FA investigates NFA with antennae.
is investigated	NFA investigates FA with antennae.
Contact, passive	FA incidentally contacts NFA.
is contacted, passive	NFA incidentally contacts FA.
Contact, sustained	FA remains in antennal or body contact >5s. with NFA.
is contacted,sustained	NFA remains in antennal or body contact >5s. with FA.
Approaches	FA approaches NFA within one bodylength.
is approached	NFA approaches FA within one bodylength.
Remains near	FA remains within one bodylength of NFA >5s.
is remained near	NFA remains within one bodylength of FA >5s.

Cricket Ethogram Behavior List continued

Chases	FA chases NFA a distance greater than one bodylength.
is chased	NFA chases FA a distance greater than one bodylength.
Supplants	FA forces off and overtakes area occupied by NFA.
is supplanted	NFA forces off and overtakes area occupied by FA.
Stands on	FA stands on NFA.
is stood on	NFA stands on FA.
Kicks	FA kicks NFA with leg(s).
is kicked	NFA kicks FA with leg(s).
Threatens	FA raises body and wings in threat display to NFA.
is threatened	NFA raises body and wings in threat display to FA.
Charges	FA charges NFA in threat display.
is charged	NFA charges FA in threat display.
Fights	FA fights head to head with NFA.
Sings, calling	FA sings loud calling song.
Sing, rivalry	FA sings rivalry song at NF male.
is sung at,rivalry	NFA sings rivalry song at F male.
Courts	FMale sings courtship song with courtship dance at NFFemale.
is courted	FFemale is sung courtship song with courtship dance by NFMale.
Oviposits	FFemale probes substrate with ovipositor.

Cricket Ethogram Behavior List continued

Mounts	FFemale climbs on top of NFmale or is moved under and is held/attempted to be held by male's cerci.
Is mounted	Fmale is climbed on top of by NFfemale or moved under and holds/attempts to hold female with his cerci.
Copulates	Fmale or Ffemale joins reproductive organs with NFmale or NFfemale.

APPENDIX C

Reliability results for the Rating of Subjective Dominance
and Observation of Observed behaviors

Subjective Dominance Ranks

Table C.1 is a full breakdown of the proportions of variance estimated in the model of subjective rankings for both the Dominance Formation (DF) period and the Stable Dominance (SD) period. Both the semipartials of the total variance and the partials of the rater and nonrater effects are given. This table provides the breakdown of interrater reliabilities across dominance periods and crickets. The estimates of classical test theory reliability can be obtained by summing the semi-partial η^2 for the estimated nonrater effects, indicating at least .733 of the total "true score" variance for the dominance formation period and .934 for stable dominance (line 3, column 3). These portions of the variance were not due to rater differences. These classical test theory results indicate that subjective dominance ranks were more variable over the dominance formation period, as would be expected since agonistic encounters are only beginning to gauge dominance attributes. The subtotals for the rater effects were .062 for the Dominance Formation and .032 for the Stable Dominance.

Table C.1

Hierarchical General Linear Model For Generalizability
Analysis of Subjective Ratings of Dominance

Source	DF	ETA ² SEMIPARTIAL	ETA ² PARTIAL
Dominance Formation			
Cricket	7	.719	.980
<u>Block</u>	<u>2</u>	<u>.015</u>	<u>.020</u>
<u>Subtotal</u>	<u>9</u>	<u>.733</u>	<u>1.000</u>
Rater	1	.009	.151
Cricket*Rater	7	.042	.670
<u>Block*Rater</u>	<u>2</u>	<u>.011</u>	<u>.179</u>
<u>Subtotal</u>	<u>10</u>	<u>.062</u>	<u>1.000</u>
Model	19	.796	
<u>Residual</u>	<u>28</u>	<u>.204</u>	
Total	47	1.000	
Stable Dominance			
Cricket	8	.925	.990
<u>Block</u>	<u>2</u>	<u>.009</u>	<u>.010</u>
<u>Subtotal</u>	<u>10</u>	<u>.934</u>	<u>1.000</u>
Rater	1	.006	.174
Cricket*Rater	8	.026	.804
<u>Block*Rater</u>	<u>2</u>	<u>.001</u>	<u>.022</u>
<u>Subtotal</u>	<u>11</u>	<u>.032</u>	<u>1.000</u>
Model	21	.966	
<u>Residual</u>	<u>32</u>	<u>.034</u>	
Total	53	1.000	

Table C.2 gives the estimated variance components for each element of the subjective ranks: crickets, blocks, and raters (obtained through PROC VARCOMP METHOD=TYPE1).

Table C.2

Estimated Variance Components For Subjective Ratings

Component	Estimate
Dominance Formation	
$\sigma^2(\text{Cr})$	0.723
$\sigma^2(\text{Blk})$	0.005
$\sigma^2(\text{R})$	0.010
$\sigma^2(\text{Cr}*\text{R})$	-0.020
$\sigma^2(\text{Blk}*\text{R})$	-0.010
$\sigma^2(\text{Error})$	0.327
Stable Dominance	
$\sigma^2(\text{Cr})$	0.995
$\sigma^2(\text{Blk})$	0.012
$\sigma^2(\text{R})$	0.006
$\sigma^2(\text{Cr}*\text{R})$	0.038
$\sigma^2(\text{Blk}*\text{R})$	-0.004
$\sigma^2(\text{Error})$	0.057

Note. Cr = cricket; Blk = Block; R = rater

Negative variance estimates are artifacts of the estimation procedure occurring when the true values of the parameters are very close to zero (Figueredo et al., 1995). The three critical variance components are $\sigma^2(\text{Cr})$, $\sigma^2 \text{Cr}(\text{Blk})$, and $\sigma^2(\text{Cr}*\text{Rater})$. Generalizability coefficients constructed using the estimated variance components from Table C.2 were as follows:

<u>FACET</u>	<u>E²_{rel} Formation</u>	<u>E²_{rel} Stable</u>
Blocks	.993	.988
Raters	.987	.994

The E²_{rel} over blocks indicates that temporal stability of the subjective ratings over the blocks within each dominance period were highly consistent. The E²_{rel} over raters indicates the interrater reliability, which also is high. These results indicate that cricket dominance ranks remained stable over time. In addition, the raters gave males the same ranks. Any differences between crickets based on ranks are due to "real" characteristics of the crickets' dominance status.

Objective Behavior Factors: Aggression and Submission

Table C.3 is a full breakdown of the proportions of variance estimated in the model of the objective factors for both the Dominance Formation and Stable Dominance periods. Both the semipartial of the total variance and the partials of the rater and nonrater effects are given. This table shows the breakdown of interrater reliabilities across dominance periods and crickets. The estimates of classical test theory reliability are .681 for the dominance formation period and .532 for stable dominance (line 12, column 3). These numbers are substantially smaller than for the subjective ranks.

Table C.3

Hierarchical General Linear Model For Generalizability
Analysis of the Objective Behavior Factors

Source	DF	$\text{ETA}^2_{\text{SEMIPARTIAL}}$	$\text{ETA}^2_{\text{PARTIAL}}$
Dominance Formation			
Factor	1	.000	.000
Behavior	16	.023	.033
Group	7	.076	.112
Cricket	24	.035	.051
Block	2	.174	.256
Gr*F	7	.002	.002
Cr*F	24	.105	.155
Blk*F	2	.002	.002
Gr*Beh	112	.056	.082
Cr*Beh	384	.183	.269
<u>Blk*Beh</u>	<u>32</u>	<u>.026</u>	<u>.038</u>
<u>Subtotal</u>	<u>611</u>	<u>.681</u>	<u>1.000</u>
Rater	1	.001	.208
Gr*R	7	.001	.322
Cr*R	24	.000	.152
Blk*R	2	.000	.018
Gr*F*R	8	.000	.041
Cr*F*R	24	.001	.257
<u>Blk*F*R</u>	<u>2</u>	<u>.000</u>	<u>.002</u>
<u>Subtotal</u>	<u>68</u>	<u>.003</u>	<u>1.000</u>
Model	679	.684	
<u>Residual</u>	<u>2776</u>	<u>.316</u>	
Total	3455	1.000	

Source	DF	<u>ETA² SEMIPARTIAL</u>	<u>ETA² PARTIAL</u>
Stable Dominance			
Factor	1	.000	.000
Behavior	16	.031	.058
Group	8	.059	.110
Cricket	24	.031	.059
Block	2	.016	.031
Gr*F	8	.004	.007
Cr*F	24	.101	.190
Blk*F	2	.000	.000
Gr*Beh	128	.077	.145
Cr*Beh	384	.197	.371
<u>Blk*Beh</u>	<u>32</u>	<u>.015</u>	<u>.028</u>
<u>Subtotal</u>	<u>629</u>	<u>.532</u>	<u>1.000</u>
Rater	1	.001	.179
Gr*R	8	.001	.266
Cr*R	24	.001	.208
Blk*R	2	.000	.002
Gr*F*R	9	.000	.145
Cr*F*R	24	.001	.197
<u>Blk*F*R</u>	<u>2</u>	<u>.000</u>	<u>.002</u>
<u>Subtotal</u>	<u>70</u>	<u>.003</u>	<u>1.000</u>
Model	699	.535	
<u>Residual</u>	<u>2864</u>	<u>.465</u>	
Total	3563	1.000	

This finding is not surprising since individual behaviors are more ambiguous than the global outcomes of multiple agonistic encounters. In addition, behaviors may have multiple functions, aggressive or submission only being

part. For example, the behavior *approaches* can be aggressive, incidental or investigatory in nature. These results show that a substantial number of *approaches* are in fact functioning as aggression. Table C.4 gives the estimated variance components of the elements of the objective behavior factors (using PROC VARCOMP METHOD=TYPE1).

Table C.4

Estimated Variance Components For Objective Behavior Factors

Component	Estimate
Dominance Formation	
$\sigma^2(F)$	-0.002
$\sigma^2(Beh)$	0.005
$\sigma^2(Gr)$	0.124
$\sigma^2(Cr)$	-0.108
$\sigma^2(Blk)$	0.296
$\sigma^2(Gr*F)$	-0.076
$\sigma^2(Cr*F)$	0.293
$\sigma^2(Blk*F)$	0.001
$\sigma^2(Gr*Beh)$	0.003
$\sigma^2(Cr*Beh)$	0.239
$\sigma^2(Blk*Beh)$	0.042
$\sigma^2(R)$	0.001
$\sigma^2(Gr*R)$	0.002
$\sigma^2(Cr*R)$	-0.001
$\sigma^2(Blk*R)$	0.000
$\sigma^2(Gr*F*R)$	0.000
$\sigma^2(Cr*F*R)$	-0.013
$\sigma^2(Blk*F*R)$	-0.002
$\sigma^2(Error)$	0.450

Component	Estimate
Stable Dominance	
$\sigma^2(F)$	-0.002
$\sigma^2(Beh)$	0.015
$\sigma^2(Gr)$	0.070
$\sigma^2(Cr)$	-0.075
$\sigma^2(Blk)$	0.019
$\sigma^2(Gr*F)$	-0.055
$\sigma^2(Cr*F)$	0.200
$\sigma^2(Blk*F)$	-0.001
$\sigma^2(Gr*Beh)$	0.012
$\sigma^2(Cr*Beh)$	0.165
$\sigma^2(Blk*Beh)$	0.013
$\sigma^2(Rater)$	0.001
$\sigma^2(Gr*R)$	0.001
$\sigma^2(Cr*R)$	0.000
$\sigma^2(Blk*R)$	0.000
$\sigma^2(Gr*F*R)$	0.001
$\sigma^2(Cr*F*R)$	-0.014
$\sigma^2(Blk*F*R)$	-0.001
$\sigma^2(Error)$	0.457

Note. F = factor; Beh = behavior; Gr = group; Cr = cricket; Blk = block; R = rater.

The three critical variance components for this study are $\sigma^2(Cr*Factor)$, $\sigma^2(Cr*Beh)$, $\sigma^2(Blk*Factor)$ and $\sigma^2(Cr*Factor*Rater)$. These are the individual differences of the crickets within the factors. The main effects were not the focal aspect of this analysis. Generalizability

coefficients constructed from the estimated variance components from Table C.4 were as follows:

<u>FACET</u>	<u>E²_{rel} Formation</u>	<u>E²_{rel} Stable</u>
Behaviors	.550	.548
Blocks	.997	1.000
Raters	1.000	1.000

The E²_{rel} over behaviors indicates the inter-item consistency of the objective factors to their constituent behaviors. These generalizability coefficients verify that the behaviors are indicative of their factor with ample reliability. The E²_{rel} over blocks indicates that the high temporal stabilities of the objective factors over the blocks within each dominance period. The E²_{rel} over raters indicates high interrater reliability.

The reliabilities between the Dominance Formation and Stable Dominance periods show what may be an unexpected decrease. The expectation is that a stable hierarchy would produce higher reliabilities in the behaviors of individual crickets than in a unstable hierarchy during its formation period. However, stable hierarchies usually also result in fewer agonistic behaviors, since overt aggression is no longer necessary to obtain dominance. In this study, behavioral occurrences decreased dramatically in the Stable Dominance condition, such that in some blocks no agonistic behaviors occurred. Such conditions reduces the power of the analyses and the end result is lower reliabilities

Appendix D

Table D.1

Estimated Variance Components for the Between-chirp Song Characteristics

Song Levels	Estimate				
	CHL	SYLN	FMIN	FMAX	ICHL
σ^2 (Cricket)	179.54	0.06	0.03	0.13	86488.02
σ^2 (Song)	422.12	0.10	0.01	0.15	213786.14

Table D.2

Estimated Variance Components for the Within-chirp Song Characteristics

Song Levels	Estimate				
	SYLL	FREQ	FREQI	SYLI	ISL
σ^2 (Cricket)	16.6	0.05	7369.6	4407130.4	25.14
σ^2 (Song (Cricket))	4.13	0.01	12707.5	-1214485.3	21.15
σ^2 (Chirp (Song))	0.44	0.01	4238.4	4407130.4	-20.78

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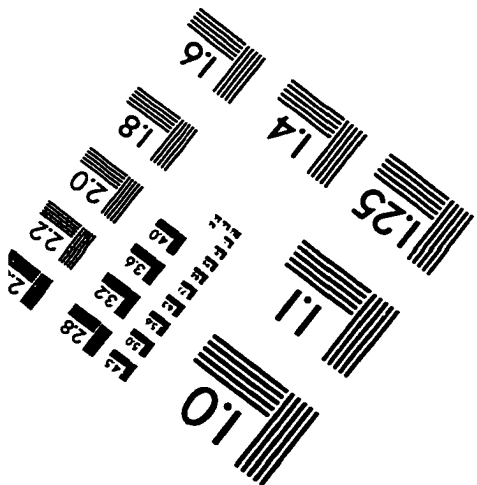
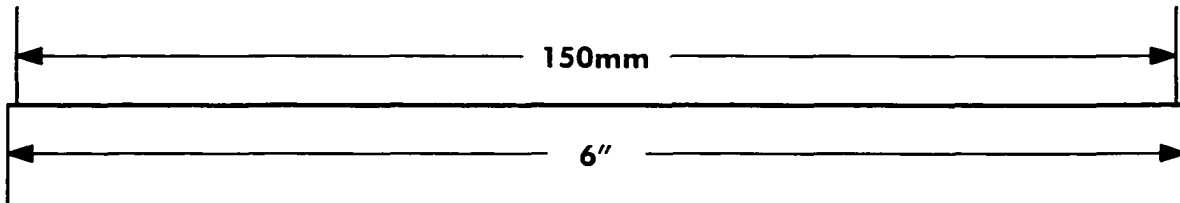
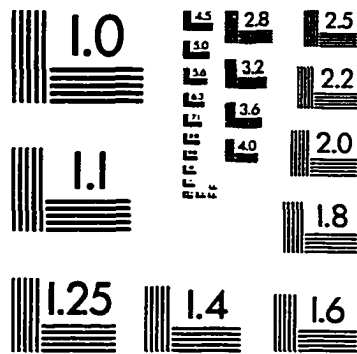
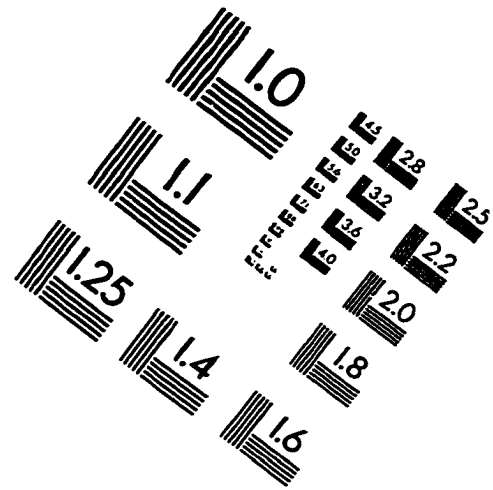
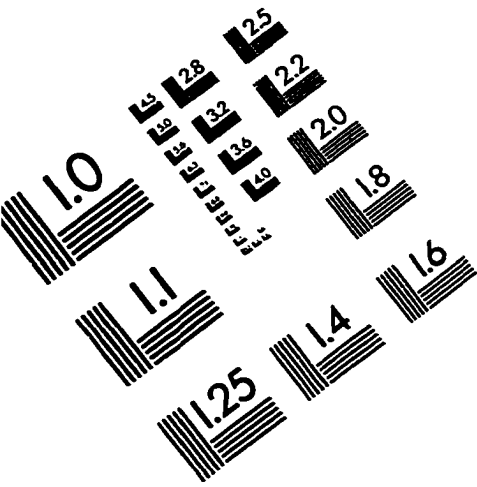
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IMAGE EVALUATION TEST TARGET (QA-3)



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